

## Revision of *Danais* Vent. (*Rubiaceae*) in Madagascar and the Comores

C. PUFF & R. BUCHNER

**Summary :** *Danais* Vent. comprises 26 species (plus some imperfectly known taxa). The genus is centred in the East Malagasy Region and the majority of species are endemic to the island. The widely distributed *D. fragrans* is the only species that extends from Madagascar to Mauritius and Réunion. *D. humblotii* occurs both in Madagascar and the Comores, and one imperfectly known species, *D. comorensis*, is known from Mayotte only (three additional taxa, two Mascarene endemics and one African mainland species, do not occur in Madagascar). A key to the species and detailed descriptions of the taxa, including data on pollen, phenology and ecology and distribution, are provided. Relationships of the taxa and certain problems in delimiting closely allied species are critically discussed. Several previously recognized species are reduced to synonymy, and three new species are described : *D. brickavillensis* Leroy ex Puff & Buchner, *D. magna* Puff & Buchner and *D. rubra* Puff & Buchner.

**Résumé :** Le genre *Danais* Vent. renferme 26 espèces (plus quelques taxons insuffisamment connus). Il est centré dans la région Est de Madagascar et la majorité des espèces sont endémiques de cette île. *D. fragrans*, largement répandu, est la seule espèce qui s'étend de Madagascar à l'île Maurice et la Réunion. *D. humblotii* se trouve à Madagascar et aux Comores, et *D. comorensis*, espèce insuffisamment connue, ne se trouve qu'à Mayotte (trois autres taxons, deux endémiques des Mascareignes et un du continent africain, ne se rencontrent pas à Madagascar). Une clé des espèces et des descriptions détaillées des taxons, avec des données palynologiques, phénologiques, écologiques et chorologiques, sont fournies. Les affinités des taxons et certains problèmes de délimitation d'espèces très apparentées sont exposés et discutés. Plusieurs espèces antérieurement reconnues sont mises en synonymie, et trois nouvelles espèces sont décrites : *D. brickavillensis* Leroy ex Puff & Buchner, *D. magna* Puff & Buchner et *D. rubra* Puff & Buchner.

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### INTRODUCTION

BUCHNER & PUFF (1993) studied in detail the character states of *Danais*, *Schismatoclada* and *Payera* (incl. *Coursiana*), a group of very closely allied Madagascar-centred genera. The analysis of the obtained data strongly suggested a redelimitation and recircumscription of the genera. As a result, a number of species were transferred from genera under which they were originally described to others. Several of these changes also involved species hitherto thought to belong to *Danais*.

Consequently, CAVACO's (1966) treatment of *Danais* is no longer valid. Moreover, due to concentrated collecting efforts in recent years, 1) additional and better material has become available of previously ill-known species (which, in part, make certain taxonomic amendments necessary), and 2) new taxa have surfaced.

The aim of the present article, therefore, is to present an up-to-date treatment of *Danais*. Efforts have deliberately been concentrated on taxa occurring in Madagascar and the Comores : the genus is centred and has the highest concentration of taxa in Madagascar, and virtually all of the taxonomic problems in *Danais* revolve around taxa occurring on the " Grand Ile " (and sometimes also the Comoro Islands). Taxa occurring elsewhere are not or only marginally dealt with because 1) they are " unproblematic " taxonomically, and 2) all of them have been studied for recent flora treatments (*D. xanthorrhoea*, the only African mainland species, for " Flora of Tropical East Africa ", and the Mascarene endemics *D. sulcata* and *D. corymbosa* for " Flore des Mascareignes " ; VERDCOURT, 1976 and 1989, respectively).

## MATERIAL AND METHODS

Material of *Danais* from the following herbaria was studied : BM, BR, K, M, MO, P, UPS, W and WU (abbreviations according to " Index Herbariorum ", HOLMGREN et al., 1990) ; a total of nearly 800 sheets was seen. Also some specimens preserved in FPA or 70 % ethanol were available. — For details on methods (SEM investigations) see BUCHNER & PUFF (1993).

Collections (under " Material Examined ") are arranged from North to South and East to West according to grid reference. As the collection listings are printouts from a computerized data bank, approximate and not fully precise grid references are given as e.g. " [S 00.00 c, E 00.00 c] " ; the latter were primarily used for collections made a) between two towns or villages, b) in large Nature Reserves, or c) around small villages which could not be traced (in that case, approx. grid references refer to the main town of the Canton in which it is located).

## SYSTEMATICS

### GENERIC DESCRIPTION

#### DANAIS Vent.

Tabl. 2 : 548 (1799).

— *Alleizettea* DUBARD & DOP, J. Bot. (Morot), sér. 2, 3 : 6 (1925). Typus generis : *Alleizettea bracteata* DUBARD & DOP ; is *D. volubilis* BAKER. - See PUFF (1991).

TYPUS GENERIS : *D. fragrans* (LAM.) PERS., Syn. Pl. 1 : 198 (1805) ; = *Paederia fragrans* COMMERS. ex LAM., Encycl. Méth. 2 : 260 (1786).

Woody lianas or climbing shrubs with branched stems to ca. 25 m long ; in a few species stems and leaves sometimes foetid when crushed. Leaves decussate or, less commonly, in whorls of 3 or 4, mostly distinctly petiolate ; leaf-blades variously shaped, thick and coriaceous

or thinnish, membranous ; stipules interpetiolar, often triangular to  $\pm$  deltoid or  $\pm$  rounded, seldom bifid, multifimbriate or with lacerate margins or with a short connate base.

Inflorescences terminal and/or axillary, variously shaped, thyrse, cymes very many- to rather few-flowered. Flowers heterodistylous, basically 5-merous. Calyx lobes small to much-elongated. Corolla tube short, funnel-shaped to long, narrowly funnel-shaped to cylindrical, base of tube often with splits, outside mostly glabrous, lobes spreading to  $\pm$  recurved ; throat often densely hairy (especially in long-styled flowers). Stamens included in long-styled flowers, anthers exerted on filiform filaments in short-styled flowers. Style filiform, with 2 filiform stigma lobes ; style and stigmas included in short-styled flowers, exerted in long-styled flowers. Ovary mostly subglobose, 2-locular, each locule with many ovules.

Fruit capsular, dehiscent loculicidally, crowned by the persistent calyx lobes. Seeds with a  $\pm$  central endosperm- and embryo-bearing part, surrounded by a thin, variously shaped wing with reticulate surface and often irregularly lacerate margin.

Pollen spheroidal to subspheroidal, 3-5-colporate, average diam. 10-26  $\mu\text{m}$  ; see BUCHNER & PUFF (1993) for further details.

**DISTRIBUTION** : Madagascar (largely confined to the East Malagasy Region ; Fig 1, A), Comoro and Mascarene Islands ; on the African mainland only in Northeast Tanzania. See BUCHNER & PUFF (1993) for further comments on distribution patterns and also on habitats.

NOTES on selected “critical” character states and the use of terms (also see BUCHNER & PUFF, 1993 for details) :

— *Winged seeds* :

Data given in the key and descriptions strictly refer to viable seeds ; seed diameters given include the wing. Great care should be taken to study viable seeds (with a well-developed,  $\pm$  central endosperm- and embryo-bearing part), as non-viable winged “pseudo-seeds ” differ both in overall size (smaller !) and also in shape and size of the seed wings.

— *Corolla tube lengths* :

Throughout, the measurements were taken from corolla tubes of open flowers only. Tube lengths of buds can yield very distorted data as, especially in the long-tubed taxa, the full tube length is only reached immediately before anthesis.

— *Corolla tube shape and heterodistyly* :

Corolla tube diameters (taken immediately below the throat) tend to be much wider in long-styled than in short-styled morphs (because in the former the anthers are included in the uppermost part of the tube). For this reason, measurements are given separately for long- and short-styled morphs.

— References to relevant figures in BUCHNER & PUFF (1993) are abbreviated as “B & P - Fig. 00” in the key and the descriptions of taxa.



Fig. 1. — Distribution of *Danais* species. — A, all taxa occurring in Madagascar and the Comores. — B, *D. rhamnifolia*. — C, *D. ligustrifolia*. — D, *D. microcarpa*. — E, *D. verticillata*. — F, *D. brickavillensis*. — In A-E the dotted line marks the border between the East and West Malagasy Region, in F the western border of the Eastern Domain of the East Malagasy Region.



*D. baccata*  
will also come at  
here

- 10'. Leaf-blades not as above, coriaceous to membranous.
- 12. Inflorescences 7- to 1-flowered, terminal and occasionally also axillary, elongated (to 10 cm long) and very lax, inflorescence main axis with 3-1 pairs of pedicellate flowers, or only with a solitary terminal flower (B & P - Fig. 3, I); pedicels 5-25(-30) mm long, often with two minute bracts (0.5 mm long) around the middle; capsules ca. 8-12 mm in diam.; seeds ca. 2.5-4 mm in diam. .... 19. *D. terminalis*
- 12'. Inflorescences never with the above combination of characters, fruits and seeds variable in size.
- 13. Inflorescences essentially terminal but often also additional inflorescences in the axils of foliage leaves below.
- 14. Flowers with pedicels to 12 mm long, inflorescences rather lax and  $\pm$  rounded, pedunculate; corolla tubes 9-20 mm long.
- 15. Peduncles 10-50 mm long, inflorescences  $\pm$  many-flowered; only in the North ..... 17. *D. nigra*
- 15'. Peduncles 7-15 mm long, inflorescences several-flowered; only in the Southeast ..... 18. *D. dauphinensis*
- 14'. Flowers with short pedicels, usually not more than 2 mm long; if pedicels longer, inflorescences not as above and/or corolla tubes shorter.
- 16. Flowers  $\pm$  few to several in subsessile clusters (peduncles  $\pm$  0) terminal on short lateral branches (and occasionally also in the axils of foliage leaves below); corolla tubes 17-19 mm long; capsules 6-13 mm and seeds 2.5-4 mm in diam. .... 22. *D. pauciflora*
- 16'. Inflorescences usually more extensive; corolla tubes 2-10 mm long; capsules 2-4.5 mm and seeds 0.6-1.2 mm in diam. (if capsules larger, 7-10 mm in diam., then seeds small, 1-2 mm in diam.).
- 17. Corolla tubes 8-10 mm long; capsules 7-10 mm in diam., seeds 1-2 mm in diam.; leaves coriaceous, the veins raised and prominent above and below ... 16. *D. tsaratananensis*
- 17'. Corolla tubes 2-8 mm long (if corolla tubes to 8 mm long, then leaves not coriaceous); capsules 2-4.5 in diam., seeds 0.6-1.2 mm in diam.
- 18. Corolla tubes 5-8 mm and lobes 2-4.5 mm long; capsules 3-4.5 mm in diam.; leaves membranous, mostly glabrous above and below ..... 7. *D. humblotii*
- 18'. Corolla tubes 2-5 mm and lobes 1.3-2.5 mm long; capsules generally smaller, 2-3.5 mm in diam.; leaves (thinly) coriaceous to  $\pm$  membranous (if membranous, at least lower surface often hairy).
- 19. Leaf-blades  $\pm$  membranous or occasionally very thinly coriaceous, (20-)40-110  $\times$  (10-)20-55 mm, glabrous above or only a few hairs on the midrib, lower surface hairy on the veins to glabrescent, venation mostly raised and prominent below, often distinctly discolored (paler below than above); corolla tubes cylindrical and  $\pm$  filiform, 2.5-5 mm long ..... 1. *D. rhamnifolia*
- 19'. Leaf-blades (thinly) coriaceous, glabrous above and below, either smaller or, if of  $\pm$  equal length, relatively narrower, neither distinctly discolored nor venation prominent below and corolla tubes more funnel-shaped, 2-4.5 mm long
- 20. Leaf-blades only to 55 mm long, length to width ratio often ca. 2:1, petioles normally 1-5 mm long, stipules to ca. 1 mm long. .... 4. *D. microcarpa*
- 20'. Leaf-blades to 110(-120) mm long, often relatively narrower (length to width ratio > 2:1), petioles 3-10 mm long, stipules 1-2(-2.5) mm long.
- 21. Corolla tubes only 2-3 mm long, rather widely funnel-shaped; calyx lobes 1-1.5 mm long ..... 3. *D. breviflora*
- 21'. Corolla tubes 3-4.5 mm long, not as widely funnel-shaped; calyx lobes to 2.5 mm ..... 2. *D. ligustrifolia*
- \* 13'. Inflorescences predominantly in the axils of foliage leaves but occasionally, in addition, also an often rather depauperate terminal inflorescence.
- 22. Leaves pubescent above and below or at least entire lower surface finely pubescent, always coriaceous.
- 23. Petioles (10-)15-30 mm long, leaf-blades 70-110  $\times$  (25-)35-60 mm; corolla tubes 4-6 mm long; flowers many in rather tight, subsessile clusters in the axils of foliage leaves ..... 12. *D. magna*

\* Careful here!

- 23'. Petioles 1.5-15 mm long, leaf-blades 15-80 × 13-50 mm; corolla tubes 5-10 mm long; several- to many-flowered, mostly distinctly pedunculate thyrses with ± congested partial inflorescences in the axils of foliage leaves (occasionally also inflorescences terminal on short to ± elongated lateral branches) ..... 10. *D. pubescens* (p.p.)
- 22'. Leaves glabrous above and below or only some hairs on the midrib below, coriaceous to membranous.
24. Capsules very woody and thick-walled..... 10. *D. pubescens* (p.p.)
- 24'. Capsules rather thin-walled. *to common on Mauritius*
25. Corolla tubes 2-4.5 mm long, calyx with a short basal tubular portion (often ca. 0.5 mm high), lobes triangular or tooth-like, mostly ca. 0.1-0.5 mm long; leaves typically thick, coriaceous..... 23. *D. fragrans*
- 25'. Corolla tubes 5-9 mm long, calyx without a short basal tubular portion, lobes 0.3-1 mm long; leaves membranous to very thinly coriaceous.
26. Leaf-blades (25-)35-70(-90) × 15-35(-40) mm, petioles 4-10 mm long; leaves predominantly decussate but occasionally also in whorls of 3; calyx lobes often 1-3 mm long; seeds 1.7-2.5(-3) mm in diam. .... 24. *D. cernua*
- 26'. Leaf-blades (55-)85-120 × (20-)30-55 mm, petioles (7-)10-20 mm long; leaves strictly decussate; calyx lobes 0.3-0.5 mm long; seeds 1-1.4 mm in diam.. 25. *D. distinctinervia*

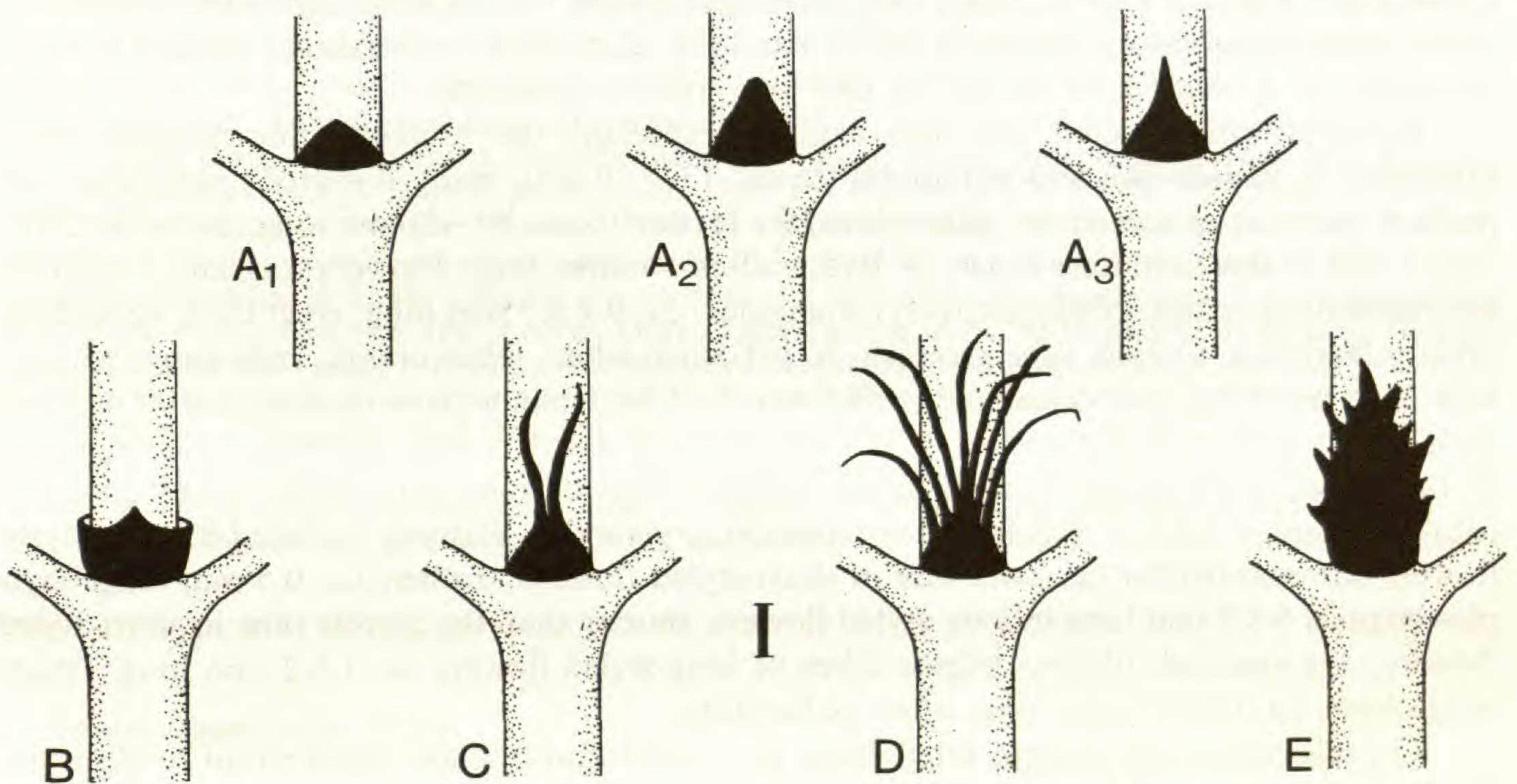


Fig. 2. — Stipule types in *Danais*. A, the most common types (A<sub>1</sub> ... A<sub>3</sub>), found in the majority of species. — B, stipule with a connate base (*D. longipedunculata*). — C, bifid stipule (*D. andribensis*). — D, multifimbriate stipule (*D. vestita*). — E, stipule with lacinate margins (*D. brickavillensis*). — Schematic (indumentum, colleters, etc. not drawn); scale bar : 1 mm (approx.).

Species 1-5 form a group of closely allied species (subsequently referred to as “*Danais microcarpa* group”) distinguished by small flowers, fruits and seeds (cf. Fig. 3 and 4) and essentially terminal inflorescences.

Species 6 might be loosely linked to the “*Danais microcarpa* group” but species 7-9, although exhibiting certain character agreements (rather small, thin-walled capsules, inflorescences), do not appear to show a very obvious and close relationship to the former.

## 1. *Danais rhamnifolia* Baker

J. Linn. Soc. (Bot.) 20 : 164 (1883); DRAKE in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : tab. 454,2 (1898); BOITEAU, Bull. Acad. Malg. 24 : 10 (1941).

— *Danais chapelieri* DRAKE, Bull. Soc. Bot. France 45 : 347 (1898, publ. 1899), in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : tab. 451A,1 (1900). Types : *Chapelier s.n.*, Madagascar, without locality (lecto-, P!; selected here); *du Petit-Thouars s.n.* (syn-, P!); *Humblot 227* (syn-, P!).

TYPE : *Baron 919*, Madagascar, "Central Madagascar" (holo-, BM!; iso-, K!, P!).

Woody lianas or climbing shrubs with branched stems to ca. 15 m long, glabrous or puberulous when young but soon glabrescent. Leaves decussate; leaf-blades  $\pm$  membranous or occasionally very thinly coriaceous, (ob)ovate to elliptic, (20-)40-110  $\times$  (10-)20-55 mm, shortly acuminate to acute, seldom  $\pm$  rounded at the apex, (gradually) narrowed to the base, glabrous above or only a few hairs on the midrib, lower surface hairy on the veins to glabrescent, venation mostly raised and prominent below, blades often distinctly discoloured (paler below than above); petioles (2-)5-12 mm long, glabrous to puberulous; stipules broadly triangular to  $\pm$  deltoid, to ca. 2(-2.5) mm long, mostly glabrous.

Inflorescences terminal and also axillary, especially the terminal inflorescences often extensive,  $\pm$  panicle-like and pyramidal (to ca. 13  $\times$  9 cm), many-flowered; peduncles and pedicels glabrous or sometimes puberulous, the former to ca. 30(-80) mm long, the latter often only 1 mm or less; ultimate bracts  $\pm$  linear, often  $<$  1 mm long. Flowers fragrant, 5-merous, heterodistylous; calyx lobes (narrowly) triangular, ca. 0.4-0.7 mm long, erect to  $\pm$  spreading, often puberulous. Corolla tube greenish- to yellowish-white, lobes orange, red-orange or red; tube 2.5-5 mm long, cylindrical and  $\pm$  filiform, ca 0.3-0.5 mm wide at the base, ca 0.5-1.3 mm wide above in short-styled and ca 0.7-1.5 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes narrowly (ob)lanceolate, 1.3-2.5  $\times$  0.5-1 mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exserted for ca. 2-4.2 mm in short-styled flowers; anthers ca. 0.5 mm long. Style plus stigmas 5-8.5 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exserted, filiform stigma lobes of long-styled flowers ca. 1.5-2 mm long. Ovary subglobose, ca. 0.3-0.7 mm long, often puberulous.

Capsule rather thin-walled, subglobose, ca. 2.5-3.5 mm in diam., glabrescent to glabrous. Seeds dark brown, 0.6-1 mm in diam., with an irregularly lacerate, sometimes  $\pm$  elongated circumferential wing. — B & P - Fig. 3, E; 11, A.

Pollen : 3(-4)-colporate; average diam. : 12-14  $\mu$ m (B & P - Fig. 15, J).

ECOLOGY AND PHENOLOGY : In eastern lowland rain forest ("forêt orientale") and also, at higher altitudes (Central Plateau), in forest with *Weinmannia* and *Tambourissa*; occasionally in disturbed, secondary sites. — Alt. : 0-1700(-2200) m. — Flowers July, February-May; fruits July, October-November, January, May-June.

DISTRIBUTION (Fig. 1, B) : Endemic to East Madagascar and occurring from the North to the extreme Southeast.



CRITICAL REMARKS : *D. rhamnifolia* is normally readily distinguished from the very close species pair *D. microcarpa*-*D. ligustrifolia* by its larger, mostly  $\pm$  membranous leaves, generally more extensive inflorescences and its flowers with typically very thin, filiform and often relatively longer corolla tubes.

As already noted by BREMEKAMP (1948), this species is very closely allied to the African mainland species *D. xanthorrhoea*.

MATERIAL EXAMINED. - MADAGASCAR : Ankaizinana [S 14.30, E 48.55], *Decary 1879* (P) ; Marojeje Res., N from Ambatoharana [S 14.31, E 49.37], *Nicoll 628* (K, MO, P) ; Imerimandroso Canton, R.N. III [S 17.26 c, E 48.35], *Réserves Naturelles Mad RN 3772* (P) ; Ambatondrazaka Distr., Manakambahiny Est, Ankasina [S 17.46, E 48.40], *Réserves Naturelles Mad RN 1912* [" 38 "] (P) ; from Manakambahiny [Est] to Nonokambo [S 17.46, E 48.42 c], *Cours 2352* (P) ; Station Alaotra [S 17.55 c, E 48.20 c], *Dequaire 27884* (P) ; Ambatohanaranana, nr. Antsevabe [S 17.58, E 48.32], *Cours 4047, 4114* (both P) ; Analamazaotra forest [S 18.56, E 48.25], *Boiteau 127 C* (P) ; Perinet, *Peltier & Peltier 3246* (P) ; Sakamaloto, *Service Forestier Mad SF 3303* (P) ; Beforona [S 18.58, E 48.35], *Decary 18026* (P) ; Ankaratra massif, Manjakatempo forest [S 19.22, E 47.18], *Humbert & Capuron 30298 bis* (P) ; Anosibe, S of Moramanga [S 19.26, E 48.13], *Decary 18462* (P) ; Ranomafana, between Fianarantsoa and Ifanadiana, 50 km E of Fianarantsoa, on Mananjary rd. [S 21.15, E 47.28], *Nicoll 108* (K, MO, P), *Phillipson 2179* (K, MO) ; Fianarantsoa Prov., Ampamaherana [S 21.26 c, E 47.05 c], *Service Forestier Mad SF 2069* (P) ; Ambalavao Dist., Vohitsaoka Canton, Antaranonby [S 22.02, E 46.43], *Réserves Naturelles Mad RN 9337* (P) ; Ivohibe Distr., Bevolombava, Antambohobe [S 22.20, E 46.47], *Réserves Naturelles Mad RN 9031* (P) ; Angondongodona [S 22.24, E 46.53], *Cours 5186* (P) ; Ivohibe [S 22.29, E 46.52], *Perrier de la Bathie 12593* (P) ; forest E of Ivohibe, *Humbert 3158* (P) ; Vohibory chain, W of Ivohibe [S 22.34, E 46.43], *Humbert 3134* (P) ; Farafangana Prov., Ivongo [S 22.30, E 47.02], *Réserves Naturelles Mad RN 7176* (P ; atypical) ; Vondrozo [S 22.49, E 47.20], *Decary 3841* (P), *5055* (BR, P) ; Benanorema [nr. Vangaindrano] [S 23.21, E 47.36], *Lantz s.n.* (P) ; Androy Distr., Esira Canton, R.N. XI [S 24.20 c, E 46.42 c], *Réserves Naturelles Mad RN 5160* (P) ; Chaines Anosyennes, Fort Dauphin - Ranamafona rd., km 1-28 from route 10 [S 24.34, E 46.55 c], *Croat 31802* (MO) ; Fort Dauphin Distr., Ifarantsa Canton, R.N. XI [S 24.56, E 46.52], *Réserves Naturelles Mad RN 2910* (P) ; Fort Dauphin [S 25.02, E 47.00], *Cloisel 203* (BM, P ; atypical), *Scott Elliot 2638* (K). — Not traced : Angalampena, *Scott Elliot 2164* (P ; atypical). — No locality given (or only "Central Madagascar") : *Baron 919* (BM, K, P), *2468* (K  $\times$  2, P) ; *Chapelier s.n.* (P) ; *du Petit-Thouars s.n.* (P) ; *Homolle 1789* (P) ; *Humblot 227* (P) ; *Lastelle s.n.* (P) ; *Prince H d'Orléans s.n.* (P).

## 2. *Danais ligustrifolia* Baker

J. Linn. Soc. (Bot.) 20 : 162 (1883) ; BOITEAU, Bull. Acad. Malg. 24 : 12 (1941).

TYPES : *Lyall 123 bis*, Madagascar, Central Madagascar [in the province of Imerina] (lecto-, K!, selected here) ; *Baron 494* (syn-, P!), *1073* (syn-, K!, P!).

Woody lianas or climbing shrubs with branched glabrous stems to ca. 25 m long. Leaves decussate ; leaf-blades (thinly) coriaceous, elliptic, obovate, ovate to lanceolate-ovate, (32-)40-100(-120)  $\times$  15-40(-45) mm, shortly acuminate to acute at the apex, cuneate to gradually narrowed to the base, glabrous above and below ; petioles 3-10 mm long, glabrous ; stipules  $\pm$  deltoid, to 2(-2.5) mm long, glabrous.

Inflorescences terminal and sometimes also some axillary inflorescences below ; the terminal inflorescences either extensive, many-flowered, rather lax and  $\pm$  (broadly) pyramidal

(to ca. 14 × 10 cm) or fewer-flowered, smaller, more compact and narrower ; peduncles and pedicels glabrous or sometimes puberulous, the former to ca. 35 mm long, the latter often only 1 mm or less ; ultimate bracts ± linear, often < 1mm long. Flowers, fragrant, 5-merous, heterodistylous ; calyx lobes (narrowly) triangular, lanceolate to almost spathuliform, ca. (0.5-)0.7-2.5 mm long, erect to ± spreading, mostly glabrous. Corolla tube (greenish-)white, lobes yellowish or orange ; tube 3-4.5 mm long, funnel-shaped, ca. 0.6-0.9 mm wide at the base, ca. 0.9-1.8 mm wide above in short-styled and ca. 1.5-2 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers ; base of tube with splits ; lobes oblong, 1.5-2 × 0.8-1 mm, ± spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. (1.5-)2-3.8 mm in short-styled flowers ; anthers ca. 0.7-0.8 mm long. Style plus stigmas 6-8 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers ; the exerted, filiform stigma lobes of long-styled flowers ca. 1-1.5 mm long. Ovary subglobose, ca. 0.5-1 mm long, mostly glabrous.

Capsule rather thin-walled, subglobose, ca. 3-3.5 mm in diam., glabrous. Seeds dark brown, 0.7-1.1 mm in diam., with an broad irregularly lacerate, sometimes ± elongated circumferential wing. — B & P - Fig. 10, C ; 11, B-D.

Pollen : 3(-4)-colporate ; average diam. : 12-15 μm.

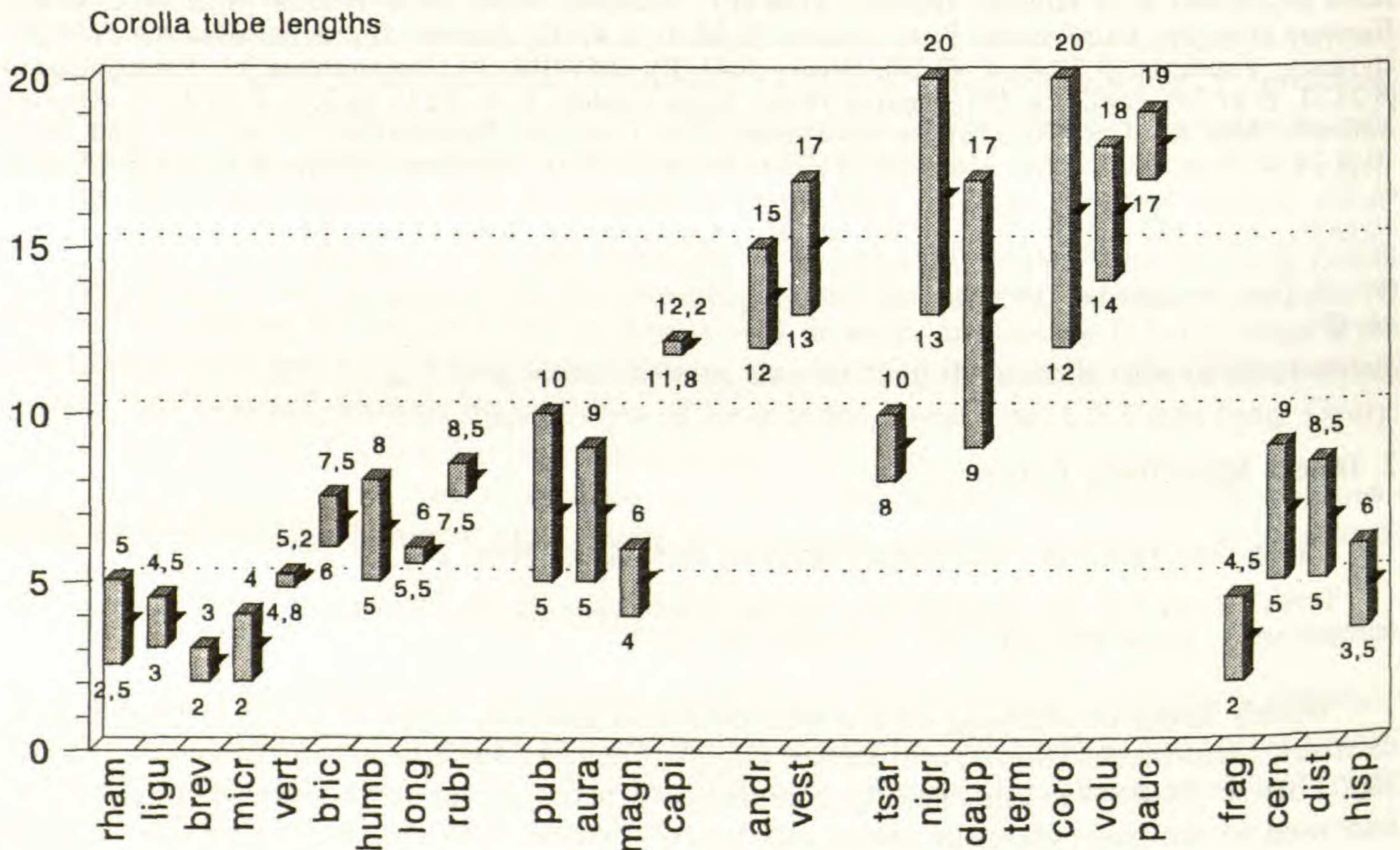
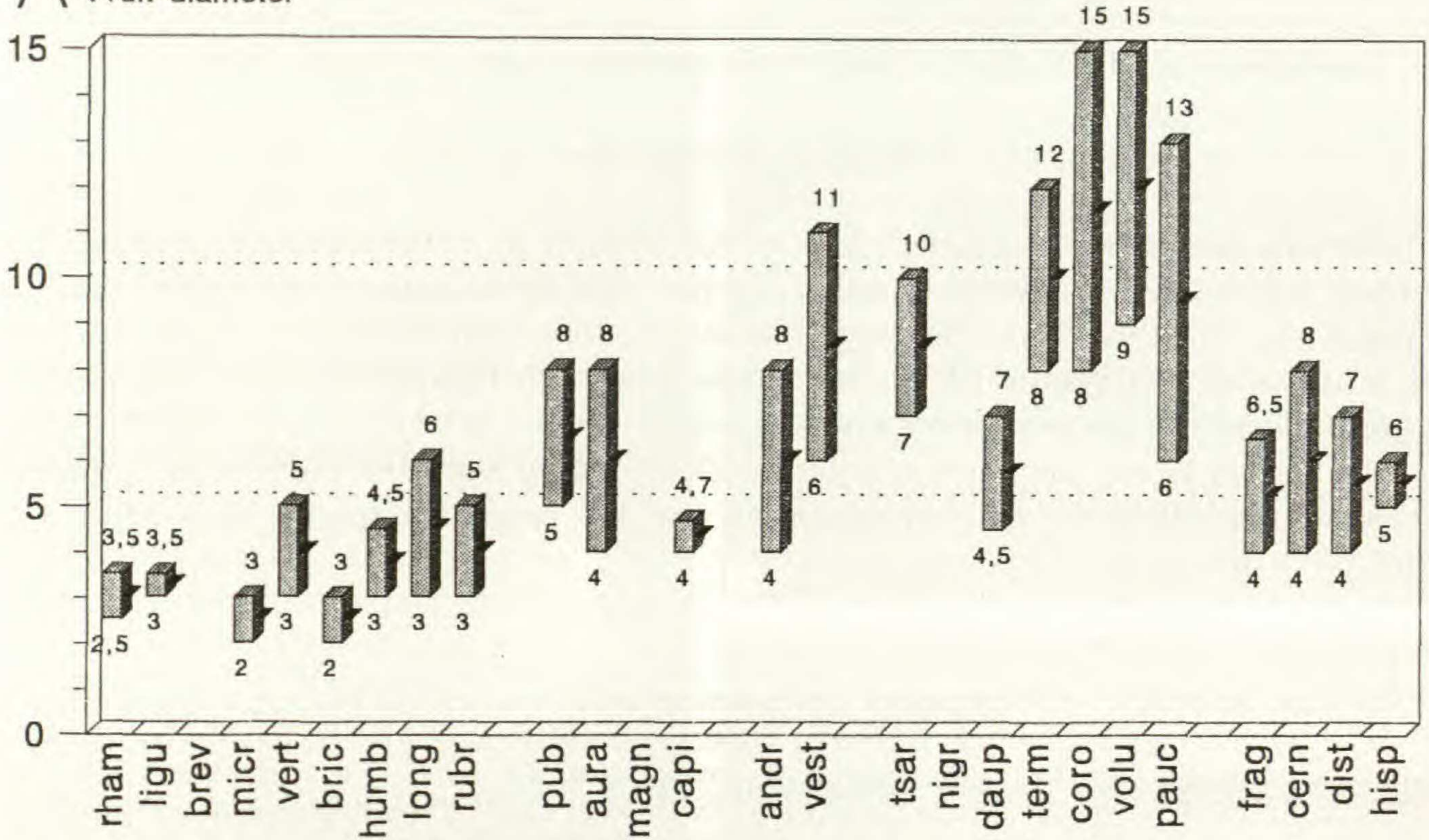


Fig. 3. — Corolla tube lengths of *Danais* species. — Minimum, maximum and average lengths in mm ; sequence of species as in the text (blanks : no data available).

**A** Fruit diameter



**B** Seed diameter

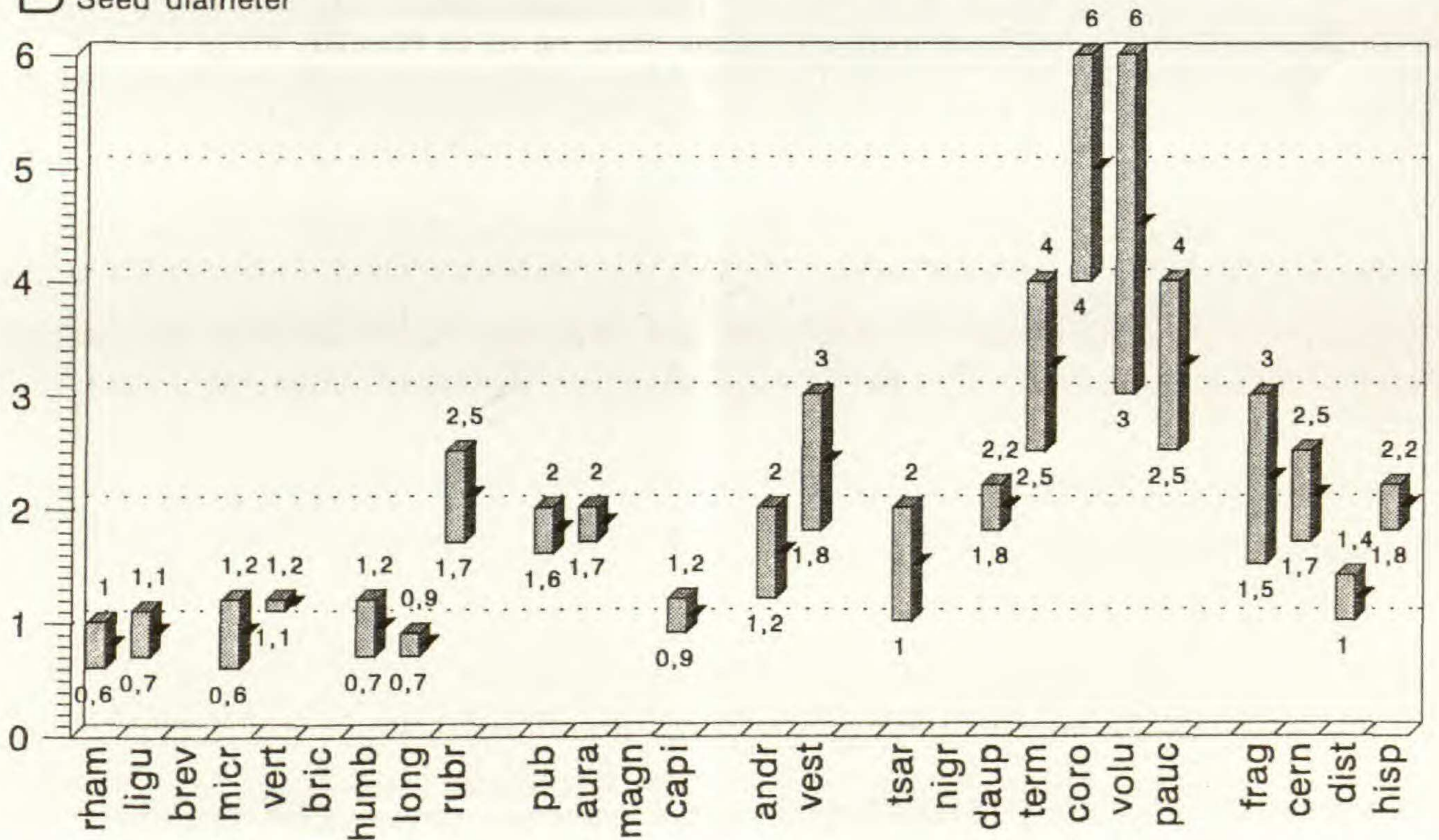


Fig. 4. — Fruit (A) and seed diameters (B) of *Danais* species. — Minimum, maximum and average lengths in mm; sequence of species as in the text (blanks : no data available).

ECOLOGY AND PHENOLOGY : Mostly in eastern lowland rain forest ("forêt orientale"), sometimes in valleys and ravines ; also in savoka vegetation. — Alt. : 0-1040 m. — Flowers July, September (October), March-June ; fruits October, February, April, June.

DISTRIBUTION (Fig. 1, C) : Endemic to Madagascar.

CRITICAL REMARKS : *D. ligustrifolia* is rather variable in its inflorescences, ranging from extensive, lax and many-flowered to rather compact and fewer-flowered, and in leaf size ; also the shape and size of the calyx lobes vary considerably. The latter, however, typically are longer than in the other members of the *D. microcarpa* group ; *D. ligustrifolia* is the only species in the group, in which the calyx lobes are occasionally almost spatuliform in shape.

The species is not only very similar to *D. breviflora* but also exhibits an undeniable and close relationship to *D. microcarpa*. — See the respective species for further comments.

MATERIAL EXAMINED. — MADAGASCAR : from Andapabe to Anosivola [S 14.13, E 49.43], *Cours* 4447, 4451 (P) ; Nosy Mangabe [S 15.30, E 49.46], *Schatz* 1608 (MO), 2730 (K, MO) ; Vavatenina Distr., Sahatavy Canton [S 17.27, E 49.00], *Réserves Naturelles Mad RN* 11347 (P) ; Didy forest [S 18.07, E 48.32], *Catat* 1740 (P ; atypical) ; around Anivorano [S 18.44, E 48.58], *Perrier de la Bâthie* 14735 (P) ; La Mandraka [S 18.55, E 47.46], *Herb. Jard. Bot. Tana* 3341 (P), *Homolle X 1* (P), *Dorr et al.* 3708 (K, MO ; approaching *D. microcarpa*) ; Analamazaotra forest [S 18.56, E 48.25], *d'Alleizette* 927 M (P), *Perrier de la Bâthie* 6932 (P ; atypical), *Viguiet & Humbert* 773 (P) ; Toamasina Prov., Andasibe (Perinet) [S 18.56, E 48.25], *Benoist* 1215 (P) ; NNW of Izouard Graphite Mine, on rd. to Mantady hill [S 18.53, E 48.28], *Lowry & Schatz* 4299 (K, MO) ; NE of Graphite Mine, *Phillipson* 2123 (K, MO) ; Antsahatsaka [Moramanga - Perinet] [S 18.58, E 48.17], *Service Forestier Mad SF* 3520 (P) ; Beforona [S 18.58, E 48.35], *Decary* 20 (P) ; Sakaleona valley [S 20.35 c, E 48.25 c], *Decary* 14191 (P), 14328 (P ; mixed with *D. humblotii*) ; Ranomafana, between Fianarantsoa and Ifanadiana [S 21.15, E 47.28], *Phillipson* 2157 (MO) ; Ampamaherana, Fianarantsoa [S 21.26 c, E 47.05 c], *Service Forestier Mad SF* 2076 (P) ; nr. Ambohimahasina [S 21.56, E 47.11], *Herb. Jard. Bot. Tana* 4524 (P) ; Ambalavao Distr., Sendrisoa Canton, R.N. V [S 22.00 c, E 46.57 c], *Réserves Naturelles Mad RN* 3073 (P). — No locality given (or only "Central Madagascar" or "Central Plateau") : *Baron* 494, 894, 5644, 6601 (all P), 1073 (K, P) ; *Hodgkin & Stansfield* 310 (K) ; *Homolle* 491 (P) ; *Humblot* 221 (K, P ; a different collection, not *Danais*, in W) ; *Lastelle s.n.* (P) ; *Lyall* 123 bis, s.n. (both K).

### 3. *Danais breviflora* Baker

J. Linn. Soc. (Bot.) 20 : 163 (1883) ; DRAKE in GRANDIDIER, *Hist. Phys. Madagascar* 36 [Hist. Nat. Pl. 6] : *tab.* 454,1 (1898) ; BOITEAU, *Bull. Acad. Malg.* 24 : 9 (1941).

TYPE : *Lyall* 225, Madagascar, [in the province of Imerina] (holo-, K!).

Presumably a climbing shrub, length of the glabrous, terete stems unknown. Leaves decussate ; leaf-blades (thinly) coriaceous, obovate, 60-110 × 25-45 mm, acute at the apex, gradually narrowed to the base, glabrous above and below ; petioles 5-10 mm long, glabrous ; stipules deltoid, ca. 1-1.8 mm long, glabrous.

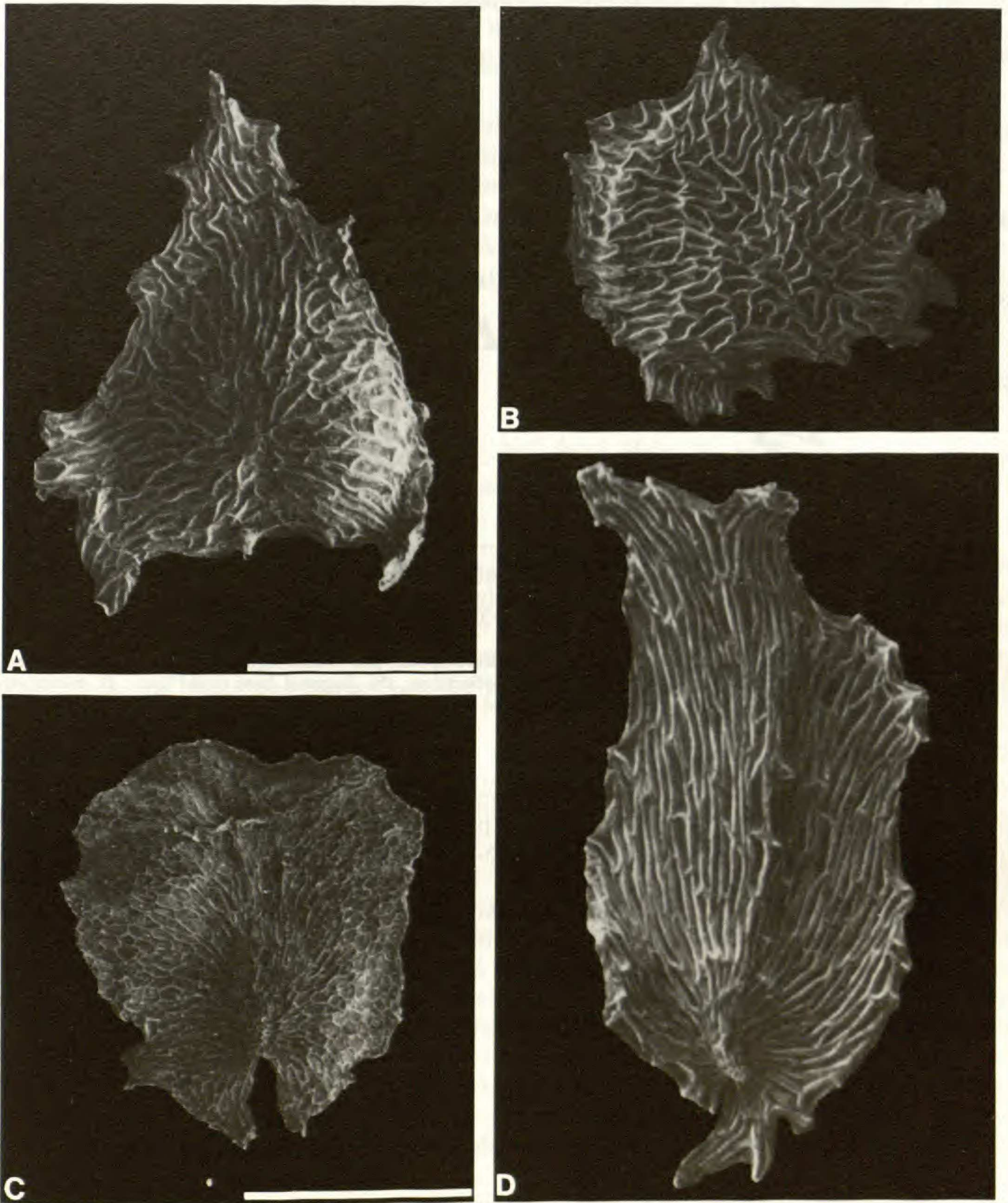


Fig. 5. Seeds of *Danais* species. — A-B, *D. microcarpa*, A, from above; B, from below (both : *Homolle 93*, P). — C, *D. vestita* (*Decary 18269*, P), from below. — D, *D. pubescens* (*Baron 1375*, P), from below. — Scale bars : 1 mm (C); 0.5 mm (A = B = D).

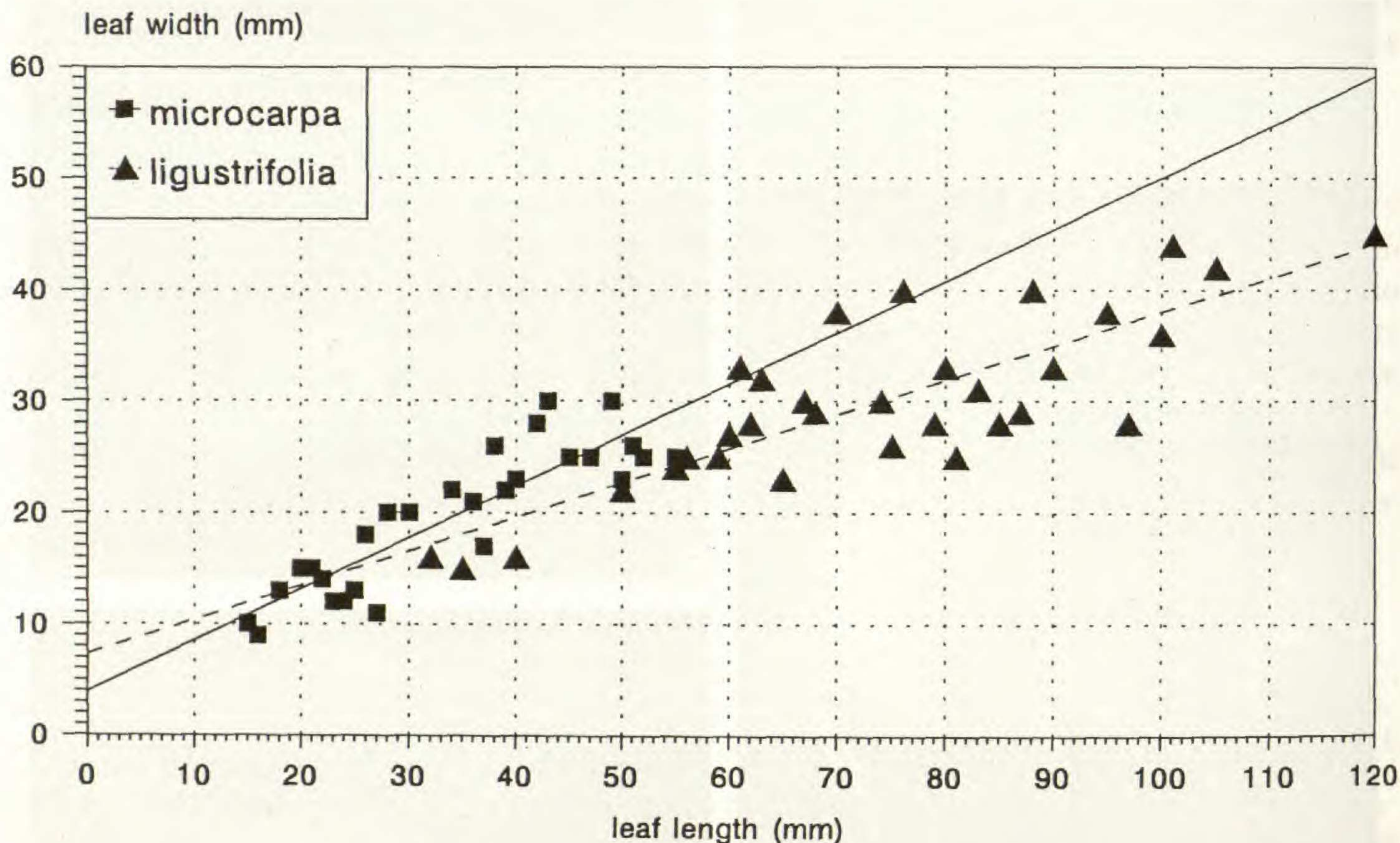


Fig. 6. — Leaf-blade lengths and widths of the closely allied species pair *Danais ligustrifolia* and *D. microcarpa*. — Lengths and widths of individual leaves of different collections; the diagonal lines (solid line : *D. microcarpa*; interrupted line : *D. ligustrifolia*) represent the averaged length to width ratios.

Inflorescences terminal and extensive, many-flowered,  $\pm$  pyramidal, ca. 90  $\times$  60 mm, axes puberulous; peduncles to 20(-30) mm long, pedicels to ca. 1 mm long; ultimate bracts linear-lanceolate, to ca. 2 mm long. Flowers 5-merous, heterodistylous; calyx lobes linear-lanceolate, ca. 1-1.5 mm, glabrous. Corolla colour unknown; tube ca. 2-3 mm long, funnel-shaped, ca. 1-1.5 mm wide at the base and ca. 1.8-2.2 mm wide above in short-styled flowers, glabrous outside, densely pilose at the throat; base of tube with splits; lobes oblong, ca. 1.5  $\times$  0.8-1 mm, glabrous outside. Stamens exerted for ca. 2 mm in short-styled flowers; anthers ca. 0.7-1 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers not seen). Ovary subglobose, < 1 mm long, glabrous.

Mature fruits and seeds unknown.

Pollen : 3-colporate; average diam. : 11-14  $\mu$ m.

ECOLOGY AND PHENOLOGY : No data available.

DISTRIBUTION : Endemic to Central Madagascar.

CRITICAL REMARKS : *D. brevipflora*, only known from the type, is originally described as a "forest shrub". BAKER may have merely guessed from the branchlets on the type sheet that

the plant is a “normal” shrub (the label bears no information on habit). In view of the fact that many other *Danais* species described by BAKER as “shrubs” or even “trees” have since been found to be *climbing* shrubs or woody lianas, it is highly probable that this also applies to *D. breviflora*.

The species is undoubtedly most closely allied to *D. ligustrifolia* and perhaps not specifically distinct. The only significant difference between the two seems to be that the only known collection of *D. breviflora* has shorter corolla and relatively wider tubes than *D. ligustrifolia* (*D. breviflora* has corolla tubes that are shorter than in any other species of the genus, cf. Fig. 3). Apart from the differing corolla tube length, several collections of *D. ligustrifolia* closely approach *D. breviflora* in their character states.

#### 4. *Danais microcarpa* Baker. — Fig. 5, A-B.

J. Linn. Soc. (Bot.) 20 : 163 (1883); BOITEAU, Bull. Acad. Malg. 24 : 13 (1941).

TYPES : *Baron 1140*, Madagascar, [forest of Andrangaloaka] (lecto-, BM!, selected here ; isolecto-, P!), *Baron 1340* (syn-, K!, P!), *Parker s.n.* (syn-, n.v.); *Bojer s.n.*, province of Betanimena (syn-, K!, W!).

Woody lianas or climbing shrubs with branched stems to ca. 5 m long, glabrous or sometimes puberulous when young but soon glabrescent. Leaves decussate ; leaf-blades (thinly) coriaceous, obovate, ovate to  $\pm$  elliptic, 15-55  $\times$  9-30 mm, shortly acuminate to acute, seldom  $\pm$  rounded at the apex, cuneate at the base or very gradually narrowed to the base, mostly entirely glabrous above and below ; petioles 1-5(-10) mm long, glabrous ; stipules  $\pm$  deltoid, usually not more than 1 mm long, glabrous.

Inflorescences terminal and also axillary, especially the terminal inflorescences often quite extensive (to ca. 8  $\times$  4 cm) and rather many-flowered,  $\pm$  cylindrical to  $\pm$  pyramidal, but sometimes also more reduced and fewer-flowered ; peduncles and pedicels glabrous or sometimes puberulous, the former to ca. 20 mm long, the latter often only 1 mm or less ; ultimate bracts  $\pm$  linear, often  $<$  1 mm long. Flowers, 5-merous, heterodistylous ; calyx lobes (narrowly) triangular, ca. 0.5-1.1 mm long, erect to  $\pm$  spreading, glabrous. Corolla tube greenish-white to yellowish-green, lobes yellowish or orange ; tube 2-4 mm long, narrowly funnel-shaped to  $\pm$  cylindrical, ca. 0.5-0.7 mm wide at the base, ca. 0.7-1.1 mm wide above in short-styled and ca. 0.9-1.4 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers ; lobes oblong, 1.5-2  $\times$  0.7-1 mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exserted for ca. 2-2.5 mm in short-styled flowers ; anthers ca. 0.7 mm long. Style plus stigmas 5-6.5 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers ; the exserted, filiform stigma lobes of long-styled flowers ca. 1 mm long. Ovary subglobose, ca. 0.5-0.9 mm long, mostly glabrous.

Capsule rather thin-walled, subglobose, ca. 2-3 mm in diam., glabrous. Seeds dark brown, 0.6-1.2 mm in diam., with an irregularly lacerate, sometimes a little elongated to  $\pm$  triangular circumferential wing.

Pollen : 3-colporate ; average diam. : 11-18  $\mu$ m.

ECOLOGY AND PHENOLOGY : In or at the edge of forest remnants of the Central Plateau, also in “dry forest of the western slopes” over gneiss and quartzite; occasionally also in remnants of eastern lowland rain forest (“forêt orientale”). — Alt. : 800-2000 m. — Flowers July-August, November-January, March, May-June; fruits July-September, December, April.

DISTRIBUTION (Fig. 1, D) : Endemic to Madagascar.

CRITICAL REMARKS : The species is sometimes difficult to distinguish from its close ally *D. ligustrifolia*. While “typical” collections of either species pose no problems (differing, inter alia, in leaf size, fruit diameter and calyx lobe length), some specimens show overlaps in certain character states such as leaves (see below), corolla tube shape and size, etc.

Leaves of *D. microcarpa* are typically smaller than those of *D. ligustrifolia*. Moreover, they normally also show a difference in the length to width ratio. *D. microcarpa* most often has leaves that are less than twice or twice as long as wide (on average, the ratio is 2 : 1), those of *D. ligustrifolia* tend to be relatively longer and narrower (length to width ratio more than 2 : 1; cf. Fig. 6).

MATERIAL EXAMINED. — MADAGASCAR : Ankaizinana forest [S 14.30, E 48.55], *Decary* 1960 (P); Ambodimanga, Anivoranotely [S 17.25 c, E 49.02], *Vigreux* 15489 (P); Zahamena, R.N. III [S 17.40 c, E 48.45 c], *Decary* 16487 (P; atypical); Lac Alaotra [S 17.50 c, E 48.25 c], *Herb. Jard. Bot. Tana* 4034 (P); Ambatondrazaka Distr., Ankaroka [S 17.50 c, E. 48.30 c], *Cours* 167 (P); Ambatohanaranana, nr. Antsevabe [S 17.58, E 48.32], *Cours* 4098 (P); Tampoketsa d'Ankazobe, P.K 181 [S 17.53 c, E 47.03 c], *Jacquemin* 1249 (P), *Decary* 19290 (P); 7 km E Anjozorobe [S 18.22, E 47.52], *Schatz et al.* 1391 (K, MO); between Fenoarivo [S 18.26, E 46.34] and Miarinarivo [S 18.47, E 46.55], *Decary* 7649 (P); La Mandraka [S 18.55, E 47.46], *Benoist* 1625 (P), *d'Alleizette* 892 M (P), *Puff, Igersheim & Rajemisoa* 850824-1/7 (TAN, WU); Toamasina Prov., Andasibe (Perinet), NE of Graphite Mine [S 18.53, E 48.28], *Phillipson* 2119 (K, MO); Analamazoatra forest [S 18.56, E 48.25], *Perrier de la Bâthie* 4005, 6906, 6929 (all P); Befoza nr. Perinet, *Service Forestier Mad SF* 2645 (P); Andrangaloaka forest [S 19.02, E 47.55], *Baron* 1140 (BM, P); Ambatolampy rd., km 39 [S 19.10 c, E 47.30], *Bosser* 6145, 6146 (both P); S of Tananarive, Iharanandriana, Behenjy [S 19.12, E 47.29], *Capuron SF* 27392 (P); Vavavato (Ankaratra) [S 19.22 c, E 47.18c], *Perrier de la Bâthie* 13943 (P); Ankaratra, Manjakatempo [S 19.22, E 47.18] *Benoist* 446, 450 (both P), *Bosser* 15257 (P); river E of Tsiafajavona, *Perrier de la Bâthie* 13542 (P); Mania basin [S 19.45 c, E 45.50 c], *Perrier de la Bâthie* 12527 (P); between Antsirabe and Ambositra, PK 238 [S 20.25 c, E 47.10 c], *Bosser* 9822 (P); around Ambatofinandrahana [S 20.33, E 46.48], *Decary* 13238 (P); between Ambatofinandrahana and Itremo [S 20.34 c, E 46.40 c], *Bosser* 9876 (P); mts. W of Itremo (W Betsileo) [S 20.35, E 46.30 c], *Humbert* 29928 (P); upper Matsiatra R., *Perrier de la Bâthie* 3916 (P); Ankafana [Tsarafidy canton] [S 21.48, E 47.15], *Deans Cowan s.n.* (BM × 2). — Not traced : Prov. Betani-mena, *Bojer s.n.* (K; W, mixed with *D. cernua*). — No locality given (or only “Central Madagascar” or “Central Plateau”) : *Baron* 1340 (K, P); *Blackburn s.n.* (K); *Campenon s.n.* (P); *Homolle* 93, 1783 (both P).

## 5. *Danais verticillata* Baker

J. Linn. Soc. (Bot.) 20 : 164 (1883); BOITEAU, Bull. Acad. Malg. 24 : 10 (1941).

TYPES : *Parker s.n.*, Madagascar, forest of Andrangaloaka (lecto-, K!, selected here); *Baron* 1307 (syn-, P!).



Presumably a climbing shrub with distinctly 4-angular, almost winged, glabrous stems ca. 1.5-2.5 m long. Leaves subsessile, strictly in whorls of 4; leaf-blades  $\pm$  membranous to thinly coriaceous, obovate to obovate-lanceolate, 30-65  $\times$  10-25 mm, shortly to long acuminate at the apex, cuneate at the base, glabrous; stipules deltoid, ca. 2-5 mm long.

Inflorescences terminal and extensive, many-flowered,  $\pm$  pyramidal, to ca. 14  $\times$  7 cm; sometimes, in addition, also smaller axillary inflorescences below; peduncles and pedicels glabrous, the former to 25 mm long, the latter ca. 1-5 mm long, thin; ultimate bracts linear-lanceolate, often  $<$  1 mm long. Flowers 5-merous, heterodistylous; calyx lobes narrowly triangular to linear-lanceolate, ca. 1 mm or less long. Corolla colour unknown; tube ca. 4-5 mm long, narrowly funnel-shaped, ca. 0.5 mm wide at the base and ca. 1 mm wide above in short-styled flowers, glabrous outside; lobes oblong, ca. 2  $\times$  0.8 mm, glabrous. Stamens exerted for ca. 2.5 mm in short-styled flowers; anthers ca. 1 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers not seen). Ovary subglobose, ca. 1 mm long, glabrous.

Capsule thin-walled, subglobose, 3-5 mm in diam., glabrous. Seeds brown, ca. 1.2 mm in diam., with an irregular, somewhat elongated circumferential wing.

ECOLOGY AND PHENOLOGY : In eastern lowland rain forest ("forêt orientale"); also in forests of the Central Plateau? - No data on altitudes and flowering and fruiting period.

DISTRIBUTION (Fig. 1, E) : Endemic to Madagascar.

CRITICAL REMARKS : *D. verticillata* is one of the most easily recognized and distinct species of the genus (leaves invariably in whorls of four; stems angular to almost winged). On account of its small flowers, fruits and seeds and terminal inflorescences it, however, undoubtedly belongs to the "*D. microcarpa* group".

The species is apparently very rare (and perhaps now extinct?). A single collection (*Cours* 4903) is the only record of *D. verticillata* from the present century.

MATERIAL EXAMINED. — MADAGASCAR : Andrangaloaka forest [S 19.02, E 47.55], *Baron* 1307 (P), *Parker s.n.* (K). — Imprecise locality : itinéraire de Didy [S 18.07, E 48.32] à Brickaville [S 18.49, E 49.04], *Cours* 4903 (P).

## 6. *Danais brickavillensis* Leroy ex Puff & Buchner, *sp. nov.* — Fig. 2, E.

— *Danais brickavillensis* LEROY, *nom. nud. in herb.*

*D. rhamnifolia affinis sed stipulis marginibus laciniatis et floribus longioribus differt.*

TYPE : *Cours* 4538, Madagascar, Brickaville Distr., Ambalarondra Canton, Andranampony to Ambodimangaroa, 23.IV.1951 (holo-, P!).

Woody lianas or climbing shrubs with branched stems to ca. 5 m long; at least younger parts densely covered with greyish to brownish long shaggy hairs. Leaves decussate; leaf-blades  $\pm$  membranous, broadly elliptic to ovate, 60-120  $\times$  25-55 mm, gradually narrowed

to the apex and to the base, rather densely covered with longish,  $\pm$  curled hairs below (especially on veins), indumentum less dense and shorter above, venation raised and prominent below; petioles 8-12 mm long, hairy; stipules rounded, mostly hairy, ca. 5-9 mm long, the margins lacinate, with several to  $\pm$  many colleter-tipped appendages to ca. 2 mm long, stipules deciduous.

Inflorescences in the axils of foliage leaves and terminal, flowers many in, at first, tightly congested,  $\pm$  globose pedunculate clusters (usually less dense in fruit); peduncles to 40 mm long, hairy, actual pedicels  $\pm$  0; bracts  $\pm$  foliaceous in the lower inflorescence portions and linear-lanceolate above, to ca. 5 mm long. Flowers 5-merous, heterodistylous; calyx narrowly lanceolate, 1-2.5 mm long, hairy,  $\pm$  erect. Corolla tube white, lobes lilac; tube 6-7.5 mm long,  $\pm$  cylindrical, ca 0.4-0.5 mm wide at the base and ca. 0.7-0.8 mm wide above in short-styled flowers, with a few hairs on the outside or  $\pm$  glabrous; lobes narrowly lanceolate, ca. 2-2.2  $\times$  0.7-0.8 mm, with a few hairs on the outside or  $\pm$  glabrous. Stamens exerted for ca. 3 mm in short-styled flowers; anthers ca. 1 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers unknown). Ovary subglobose, ca. 0.8-1 mm long, hairy.

Capsule  $\pm$  thin-walled, subglobose, 2-3 mm in diam., sometimes somewhat compressed laterally, glabrescent to glabrous. Seeds unknown.

ECOLOGY AND PHENOLOGY : In savoka in the eastern lowland rain forest ("forêt orientale") area; no further detailed information available. — Alt. : presumably < 100 m. — Flowers April; fruits June.

DISTRIBUTION (Fig. 1, *F*) : Endemic to East Madagascar.

CRITICAL REMARKS : This apparently quite rare species (only known from one flowering and one fruiting collection) is unusual in the structure of its stipules (Fig. 2, *E*; unique in the genus).

Its placement in the *D. microcarpa* group is somewhat debatable : while the small fruits support a placement in the group and the habit suggests a position possibly  $\pm$  near *D. rhamnifolia*, it differs from *D. microcarpa* and its closest allies not only in its stipules (see above) but also in its characteristic stem and leaf indumentum and in its longer corolla tubes.

MATERIAL EXAMINED. — MADAGASCAR : Brickaville Distr., Ambalarondra Canton, Andranampony to Ambodimangaroa [S 18.27, E 49.01], *Cours 4538* (P); Sakaleona valley [S 20.35 c, E 48.25 c], *Decary 14198* (P).

## 7. *Danais humblotii* ["humbloti"] Homolle

Not. Syst. (Paris) 5 : 283 (1936); BOITEAU, Bull. Acad. Malg. 24 : 10 (1941).

TYPES : *Humblot 172*, Comoro Isl., without locality (lecto-, P!, selected here; isolecto-, BM!, K!)<sup>1</sup>; *Perrier de la Bâthie 3850*, Madagascar, Manongarivo massif (syn-, P!).

1. HOMOLLE erroneously gives "1172" as collection number.

Woody lianas or climbing shrubs with branched stems to ca. 8 m long, glabrous or less often puberulous when young; stems and leaves sometimes foetid when crushed. Leaves decussate; leaf-blades membranous, ovate (-lanceolate), elliptic or sometimes obovate, 55-110 × (20-)25-45(-60) mm, acute to long acuminate at the apex, (gradually) narrowed to the base, glabrous above and below or, seldom, some hairs on the midrib below; petioles 3-12(-20) mm long, mostly glabrous; stipules triangular to ± deltoid, ca. 1-2 mm long, glabrous.

Inflorescences terminal but often also some smaller axillary inflorescences below, especially the terminal inflorescences often extensive and rather many-flowered, rounded to broadly pyramidal (to ca. 8 × 8 cm), not uncommonly broader than high; peduncles and pedicels glabrous, the former to ca. 30 mm long, the latter ca. 0.5-2 mm long; ultimate bracts ± linear, often < 1 mm long. Flowers, 5-merous, heterodistylous; calyx sometimes with a short, indistinct basal tubular part, lobes narrowly to ± broadly triangular, ca. 0.5-1.1 mm long, ± erect to spreading, glabrous or margins with short hairs. Corolla tube greenish or greenish-brown, lobes orange or red; tube 5-8 mm long, narrowly funnel-shaped to ± cylindrical, ca 0.4-0.8 mm wide at the base, ca. 0.8-1.4 mm wide above in short-styled and ca. 1.2-1.6 mm in long-styled flowers, outside glabrous, ± densely pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes oblong, 2-4.5 × 0.8-1.2 mm, ± spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. 3.5-5 mm in short-styled flowers; anthers ca. 1-1.6 mm long. Style plus stigmas 7-10 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2-3 mm long. Ovary subglobose, ca 0.7-1.2 mm long, glabrous.

Capsule rather thin-walled, subglobose, ca. 3-4.5 mm in diam., glabrous. Seeds dark brown to blackish, 0.7-1.2 mm in diam., with an irregularly lacerate circumferential wing. — B & P - Fig. 3, F-G.

Pollen : 3-colporate; average diam. : 12-16 μm.

ECOLOGY AND PHENOLOGY : In eastern lowland rain forest (“forêt orientale”) and also, at higher altitudes (Central Plateau), in forest with *Weinmannia* and *Tambourissa* and in montane cloud forest; sometimes in secondary vegetation such as savoka. — Alt. : (?0-)500-1400 m. — Flowers April-October; fruits May-August, November.

DISTRIBUTION (Fig. 7, A) : Endemic to Madagascar and the Comoro Islands.

CRITICAL REMARKS : Although rather widely distributed, *D. humblotii* is only moderately variable in characters of both the vegetative and fertile region; collections from the Comores do not exhibit any significant differences to those from Madagascar.

The species is well distinguished by the character combination essentially terminal, frequently quite extensive and many-flowered inflorescences, small fruits and seeds, and rather thinnish leaves. It may be loosely linked to the *D. microcarpa* group but there are certain disagreements (notably its longer corolla tubes).



Fig. 7. — Distribution of *Danais* species. — A, *D. humblotii*. — B, *D. longipedunculata* and *D. rubra* (\*). — C, *D. capituliformis*. — D, *D. aurantiaca*. — E, *D. magna*. — F, *D. pubescens*. — In A-D and F the dotted line marks the border between the East and West Malagasy Region, in E the western border of the Eastern Domain of the East Malagasy Region.

MATERIAL EXAMINED. — COMORES : Grande Comore, *Boivin s.n.* (P), *Doutrelepont 1099* (BR); Anjouan, *Benson s.n.* (BM), *Lavanchie s.n.* (P). — No locality given : *Humblot 172* (BM, K, P). — MADAGASCAR : Massif de Manongarivo [S 14.00 c, E 48.25 c], *Perrier de la Bâthie 3850* (P); Bealanana Distr., Mangindrano, R.N. IV [S 14.15 c, E 48.58 c], *Réserves Naturelles Mad RN 5270* (P); Tsaratanana Massif, from Mangindrano to Maromokotro, *Gentry 11583* (MO); Tamatave Distr., Ambodiriana Canton [S 17.56, E 49.17], *Réserves Naturelles Mad RN 8971* (P); Itinéraire de Didy [S 18.07, E 48.32] à Brickaville [S 18.49, E 49.04], *cours 4914* (P); La Mandraka (ca. 22 km E of Manjakandriana) [S 18.55, E 47.46], *Puff, Igersheim & Rajemisoa 850824-1/9* (TAN, WU); Moramanga Distr., Lakato [S 18.57, E 48.13], *Decary 18198* (P); S of Moramanga, *Decary 18417* (P); Anosibe Canton [S 19.26, E 48.13], *Réserves Naturelles Mad RN 8022* (P); Sakaleona valley [S 20.35 c, E 48.25 c], *Decary 14209, 14299* (both P), *14328* (P, mixed with *D. ligustrifolia*); Ranomafana, between Fianarantsoa and Ifanadiana, 50 km E of Fianarantsoa, on Mananjary rd. [S 21.15, E 47.28], *Nicoll 103* (K, MO, P), *Phillipson 2180* (K, MO); Fianarantsoa, Ampamaherana [S 21.26 c, E 47.05 c], *Service Forestier Mad SF 2083* (P). — Not traced : Prov. Betani-mena, *Bojer s.n.* (K, M, W). — No locality given : *Bojer s.n.* (W); *Service Forestier Mad SF 2620* (P).

8. **Danais longipedunculata** Homolle. — Fig. 2, B.

Not. Syst. (Paris) 5 : 285 (1936); BOITEAU, Bull. Acad. Malg. 24 : 8 (1941) [as “*Danais pedunculata*”].

TYPE : *Perrier de la Bâthie 6930*, Madagascar, Analamazaotra (holo-, P!).

Woody lianas or climbing shrubs with much-branched glabrous stems ca. 3 (-?) m long. Leaves decussate; leaf-blades coriaceous, oblanceolate, obovate to  $\pm$  elliptic, 80-135  $\times$  30-70 mm, abruptly acuminate or  $\pm$  rounded at the apex, (gradually) narrowed to the base, glabrous above and below; petioles 10-20 mm long, glabrous; stipules connate, forming a continuous sheath ca. 1 mm high (also often visible on older parts where leaves have already fallen), with triangular to  $\pm$  deltoid appendages to ca. 1.5 mm long, glabrous.

Inflorescences mostly axillary and often paired in the axils of foliage leaves, sometimes also terminal, several- to many-flowered and often rather lax, rounded to  $\pm$  pyramidal, individual inflorescences to ca. 14  $\times$  9 cm, peduncles to 100 mm long, glabrous; pedicels to ca. 2 mm long; ultimate bracts minute,  $\pm$  linear, often < 1 mm long. Flowers 5-merous, heterodistylous; calyx sometimes with a short, indistinct basal tubular part, lobes triangular to  $\pm$  deltoid, ca. 0.5-0.8 mm long,  $\pm$  erect to spreading, mostly glabrous. Corolla tube greenish-white, lobes orange or red; tube 5.5-6 mm long, narrowly funnel-shaped to  $\pm$  cylindrical, ca. 0.4-0.5 mm wide at the base, ca. 0.7-1 mm wide above in short-styled and to ca. 1.2 mm in long-styled flowers, outside glabrous,  $\pm$  densely pilose in the throat, particularly in long-styled flowers; lobes  $\pm$  linear-lanceolate, 2-3  $\times$  0.8-1 mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exserted for ca. 3.5-4 mm in short-styled flowers; anthers ca. 1-1.3 mm long. Style plus stigmas 6-9 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exserted, filiform stigma lobes of long-styled flowers ca. 2.5 mm long. Ovary subglobose, ca. 0.6-0.8 mm long, glabrous.

Capsule mostly rather thin-walled, subglobose, ca. 3-6 mm in diam., glabrous. Seeds dark brown to blackish, 0.7-0.9 mm in diam., with an irregularly lacerate, sometimes a little elongated circumferential wing.

ECOLOGY AND PHENOLOGY : In or at the edge of evergreen forest. — Alt. : 150-1200 m. — Flowers October-January, March ; fruits March, July.

DISTRIBUTION (Fig. 7, B) : Endemic to East Madagascar.

CRITICAL REMARKS : The species is vegetatively easily recognized by its characteristic stipules (Fig. 2, B) which are unique in the genus (*M<sup>me</sup> HOMOLLE* apparently overlooked this character). These, in combination with the thick, coriaceous leaves and the inflorescences with their long peduncles, provide a very good set of characters to distinguish *D. longipedunculata* from any other *Danais* species.

MATERIAL EXAMINED. — MADAGASCAR : Vavatenina Distr., Sahatavy Canton [S 17.27, E 49.00], *Réserves Naturelles Mad RN 9832* (P) ; mt. S of Fotsialanana [S 17.46, E 48.56], *Jacquemin 211* (P) ; from Fotsialana to Manak[ambahiny] Est and Ampitanoka, *Cours 2628* (P) ; Ambatohanaranana, nr. Antsevabe [S 17.58, E 48.32], *Cours 4054* (P) ; Analamazaotra [S 18.56, E 48.25], *Perrier de la Bâthie 6930* (P) ; Farafangana, Amporoforo [S 21.29, E 47.47], *Service Forestier Mad SF 13903* (P) ; Esetra forest [S 24.28, E 47.12], *Jacquemin 1176* (P) ; 22 km N Ifarantsa and 33 km N of highway 13, border of R.N. XI (Andohahela) [S 24.47, E 46.52], *Schatz & Nicoll 1264* (BR, K, MO, P). — No locality given : *Homolle 1733* (P).

### 9. *Danais rubra* Puff & Buchner, *sp. nov.* — Fig. 8, A-C.

*P. humblotii affinis sed foliis coriaceis nervulis reticulatis et seminibus majoribus differt.*

TYPE : *Gentry 11740*, Madagascar, road from Antsohihy to Bealanana, 21-23 km E of Antsahabe, 14.V.1974 (holo-, MO!).

Woody lianas or climbing shrubs with branched glabrous stems, length of stems unknown. Leaves decussate ; leaf-blades coriaceous, obovate to ovate, 40-115 × 20-55 mm, shortly acuminate at the apex, cuneate at the base, glabrous, reticulate venation pattern prominent above and below ; petioles 5-14 mm long, glabrous ; stipules triangular, ca. 1 mm long, glabrous.

Inflorescences terminal (and usually also a few smaller axillary inflorescences immediately below), many-flowered and extensive, ± rounded, broader than high, the best developed to ca. 5 × 10 cm ; peduncles and pedicels glabrous, the former to ca. 50 mm long, the latter 1 mm or less long ; ultimate bracts ± linear, often < 1 mm long. Flowers 5-merous, heterodistylous ; calyx lobes triangular, ca. 0.5-0.7 mm long, ± erect to spreading, margins with short hairs or glabrous. Corolla red ; tube 7.5-8.5 mm long, narrowly funnel-shaped to ± cylindrical, ca. 0.6-0.7 mm wide at the base, ca. 0.7-1.2 mm wide above in short-styled flowers, outside glabrous ; lobes oblong, 2-2.4 × 0.8-1 mm, ± spreading, glabrous. Stamens exerted for ca. 3-3.5 mm in short-styled flowers ; anthers ca. 1.3-1.6 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers unknown). Ovary subglobose, ca. 1 mm long, glabrous.

Capsule rather thin-walled, subglobose, ca. 3-5 mm in diam., glabrous. Seeds dark brown, 1.7-2.5 mm in diam., with an irregularly lacerate, sometimes ± elongated circumferential wing.

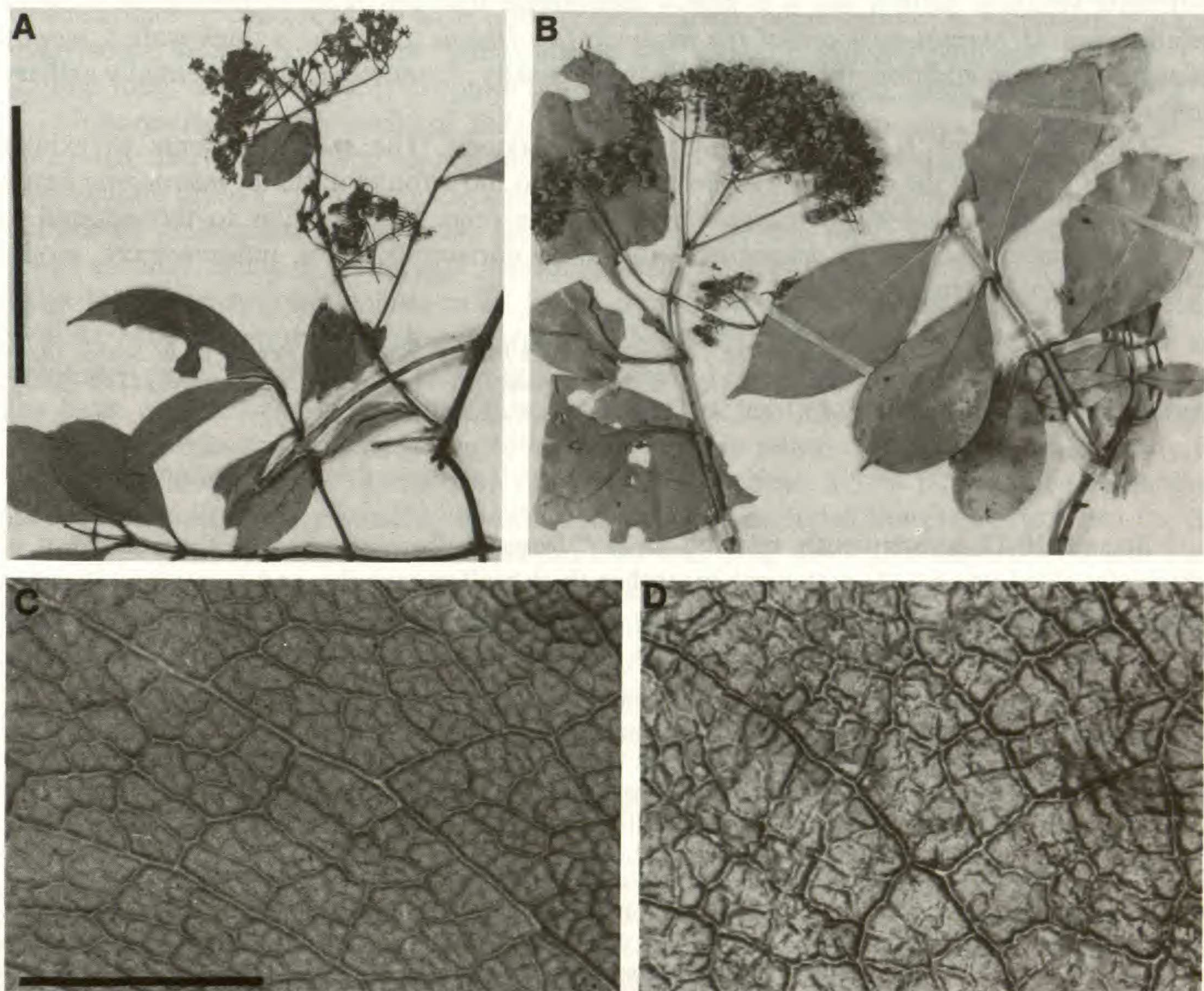


Fig. 8. — A-C, *Danais rubra*; A, portion of holotype (*Gentry 11740*, MO); B, fruiting specimen and C, reticulate venation pattern of the lower leaf-blade surface (both *Herb. Jard. Bot. Tana 5429*, P). — D, *D. aurantiaca*, as C, but upper surface (*Gentry 11271*, MO). — Scale bars : 10 cm (A = B); 1 mm (C = D).

ECOLOGY AND PHENOLOGY : In or at the edge of evergreen forest. — Alt. : 1200-2000 m. — Flowers April-May ; fruits October.

DISTRIBUTION (Fig. 7, B) : Endemic to North Madagascar.

CRITICAL REMARKS : The species is distinguished by the coriaceous leaves with their prominent reticulate venation pattern (Fig. 8, C) and the essentially terminal inflorescences. Its relationships are not entirely clear. Inflorescences, flowers and thin-walled fruits remind of *D. humblotii*, but the latter has thin leaves and the smaller seeds (cf. Fig. 4, B).

As documented in Fig. 8, *D. D. aurantiaca* shares with *D. rubra* a similarly prominent reticulate venation pattern but it is highly improbable that this is an expression of a closer relationship. *D. aurantiaca* is one of the relatively few *Danais* species with thick-walled, woody capsules which, in addition, the are partially fused basally ; it, moreover, has essentially axillary inflorescences.

The alliances of *D. rubra* are not fully understood. The species appears to exhibit characters which, on the one hand, are in agreement to those found in the *D. microcarpa* group (notably the small, thin-walled capsules) and, on the other hand, similar to those found in *D. tsaratananensis* and/or *D. dauphinensis* (distinctly coriaceous leaves, inflorescences, moderately long corolla tubes).

MATERIAL EXAMINED. — MADAGASCAR : Tsaratanana [S 14.00 c, E 49.00c], *Perrier de la Bâthie* 16284 (P) ; from Antsohihy to Bealanana, 21-23 km E of Antsahabe [S 14.47, E 48.31], *Gentry* 11740 (MO) ; Befandriana, Antsakoamahia [S 15.16, E 48.32], *Herb. Jard. Bot. Tana* 5429 (P).

Species 10-12 (subsequently referred to as “*Danais pubescens* group”) form a group of obviously allied species characterized by rather thick-walled capsules and typically pubescent stems and leaves.

Species 13 may link up with this group.

#### 10. *Danais pubescens* Baker. — Fig. 5, *D.*

J. Linn. Soc. (Bot.) 20 : 164 (1883) ; BOITEAU, Bull. Acad. Malg. 24 : 11 (1941).

— *Danais pubescens* BAKER fa. *glabra* CAVACO, *Adansonia*, sér. 2, 8 : 387 (1968). Type : *Hildebrandt* 3809, Madagascar, Imerina, Ifanangvávana hill (holo-, P! ; iso-, BM!, K!, W!, WU!).

— *Danais pubescens* BAKER fa. *brevipetiolata* CAVACO, *Adansonia*, sér. 2, 8 : 387 (1968). Types : *Decary* 6967, Madagascar, S of Moramanga (syn-, K!, P!) ; *Cours* 2010, Analamihilana forest (syn-, P!) ; *Cours* 2330, Andringitra massif, Ambodipaiso forest near Antsoabe, around Manak West (syn-, P!) ; *Cours* 2659, between Ananohambo and Manak[ambahiny] Est (syn-, P!) ; *Cours* 4449, from Andapabe to Anosivola (syn-, P!) ; *Homolle* 802, without locality (syn., P!).

— *Danais nummularifolia* BAKER, J. Linn. Soc. (Bot.) 22 : 481 (1887) ; BOITEAU, Bull. Acad. Malg. 24 : 11 (1941). Types : *Baron* 3657, Madagascar, without locality (lecto-, P!, selected here) ; *Baron* 3841 (syn-, P!).

— *Danais argentea* CAVACO, *Adansonia*, sér. 2, 8 : 386 & pl. 2, 1-4 (1968). Type : *Perrier de la Bâthie* 18341, Madagascar, Mandraka (holo-, P! ; iso-, P!).

— “*Danais paludosa* BAKER”, *nom. nud*<sup>1</sup>.

TYPES : *Parker s.n.*, Madagascar, forest of Andrangaloaka (lecto-, K!, selected here) ; *Baron* 1375, [top of Ifody mountain] (syn-, P!).

Woody lianas or climbing shrubs with branched stems to ca. 10 m long, mostly pubescent or puberulous at least when young. Leaves decussate ; leaf-blades coriaceous, variable in size, shape and indumentum, mostly ovate, obovate or orbicular, 15-80 × 13-50 mm, rounded, with

1. In his key to *Danais*, CAVACO [Bull. Mus. Hist. Nat. Paris, sér. 2, 37 : 719 (1966)] includes “*Danais paludosa*” without giving an authorship. Several sheets in herbarium P are revised by CAVACO as “*Danais paludosa* BAKER”, a name which however was never published by BAKER.



a blunt tip or indistinctly and very shortly acuminate at the apex, mostly rounded to  $\pm$  cordate or sometimes  $\pm$  cuneate at the base, pubescent above and below but not too uncommonly also glabrescent, occasionally a few hairs only on the veins or entirely glabrous; petioles 1.5-15 mm long, often pubescent; stipules triangular, ca. 1-3 mm long, often pubescent.

Inflorescences in the axils of foliage leaves, occasionally also terminal on short to  $\pm$  elongated lateral branches, comprised of several- to many-flowered, mostly distinctly pedunculate thyrses, ultimate inflorescence elements congested, all parts often pubescent, less commonly glabrescent to glabrous; peduncles to ca. 20 mm long; pedicels often  $< 1$  mm long; ultimate bracts  $\pm$  linear,  $< 1$  mm long, often hairy. Flowers 5-merous, heterodistylous; calyx lobes narrowly lanceolate, to ca. 1 mm long, erect to  $\pm$  spreading, mostly pubescent. Corolla tube brownish, greyish or purplish, lobes yellow, light orange, orange, salmon- or coral-red; tube 5-10 mm long, narrowly funnel-shaped to  $\pm$  cylindrical, ca. 0.5-1 mm wide at the base, ca. 1-1.2 mm wide above in short-styled and ca. 1.2-2 mm in long-styled flowers, outside glabrous or, occasionally, a little hairy, densely pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes lanceolate,  $3-5 \times 1-1.5$  mm,  $\pm$  spreading, glabrous or a little hairy outside. Stamens included in long-styled flowers but exerted for ca. 3-4 mm in short-styled flowers; anthers ca. 1.5-2 mm long. Style plus stigmas 8-11 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2-3 mm long. Ovary subglobose, ca. 1 mm long, pubescent or glabrous.

Capsule very woody and thick-walled, subglobose, ca. 5-8 mm in diam., glabrous. Seeds dark brown, 1.6-2 mm long or in diam., with an irregularly lacerate, often  $\pm$  elongated and asymmetrical circumferential wing.

Pollen : 3-colporate; average diam. : 12-18  $\mu$ m.

ECOLOGY AND PHENOLOGY : In or at the edge of forest remnants of forest patches in protected gullies (Central Plateau), sometimes in disturbed sites; occasionally also in eastern lowland rain forest ("forêt orientale"). — Alt. : 500-1600 m. — Flowers October-March, May-June; fruits from all year round except November and March.

DISTRIBUTION (Fig. 7, F) : Endemic to Madagascar. Rather widely distributed and occurring from the Northeast to the extreme Southeast (Fort Dauphin Distr.).

CRITICAL REMARKS : The species exhibits considerable variation in leaf size, shape and indumentum : "*D. nummularifolia*" refers to small-leaved forms (leaves not more than 15-20  $\times$  13-15 mm, petioles only ca. 1.5 mm long), "forma *glabra*" to glabrescent and "forma *brevipetiolata*" to short-petioled forms. As all these forms are connected by intermediate collections, it seems hardly worthwhile to formally uphold *D. nummularifolia* and the "forms" of *D. pubescens*. Due to the wide range of variation and overlap in several character states it was, furthermore, found impossible to maintain *D. pubescens* and *D. argentea* as separate species.

*D. pubescens* is undoubtedly rather closely allied to *D. aurantiaca* (see there for further comments).

MATERIAL EXAMINED. — MADAGASCAR : from Andapabe to Anosivola [S 14.13, E 49.43], *Cours 4449* (P) ; [E of] Lac Alaotra, between Menasaka and Ambodiriana, along Maningory R. [S 17.20, E 48.50], *Homolle s.n.* (P) ; Ambatondrazaka Distr., Imerimandroso Canton [S 17.26, E 48.35], *Réserves Naturelles Mad RN 10877* (P) ; Manaka[mbahiny] Est [S 17.46, E 48.40], *Réserves Naturelles Mad RN 6971, 10516, 11036* (all P) ; between Ananohambo and Manak[ambahiny] Est, *Cours 2659* (P) ; Ambatondrazaka [S 17.50, E 48.25], *Service Forestier Mad [Capuron] SF 1732* (P) ; Lac Alaotra [S 17.50 c, E 48.25 c], *Herb. Jard. Bot. Tana 3867, 3872* (both P) ; 47 km N of Ankazobe [S 18.05 c, E 47.10 c], *Gentry 11430* (MO) ; Tampoketsa d'Ankazobe, 5-12 km E of highway 31 km N of Ankazobe [S 18.12, E 47.17], *Gentry 11842* (MO) ; Anjozorobe, Manganibe Canton [S 18.22, E 47.52], *Boiteau 287* (P) ; Manjuga Prov., ca. 3-5 km NW Ambohitsaratelo-Bebao (NW Tsiroanomandidy) [S 18.46, E 46.02], *Barnett et al. 365* [P (ex MO)] ; Antananarivo, ca. 5 km NW of Ambohitsaratelo-Bebao (NW Tsiroanomandidy) [S 18.46, E 46.02], *Dorr 3618* (K, MO) ; La Mandraka [S 18.55, E 47.46], *Barnett et al. 447* (MO, P), *Bosser 14249* (P), *Herb. Jard. Bot. Tana 2544, 3344, 3696, 4470* (all P), *Perrier de la Bâthie 18341* (P) ; ca. 22 km E of Manjakandriana, *Puff, Igersheim & Rajemisoa 850824-1/8* (TAN, WU) ; PK 69, route Antananarivo-Toamasina [S 18.55, E 47.56], *Barnett & Dorr 203* (K, MO) ; Analamazaotra [S 18.56, E 48.25], *d'Alleizette 895 M* (P) ; S of Moramanga [S 18.57, E 48.13], *Decary 6967* (K, P) ; Andrangaloaka forest [S 19.02, E 47.55], *Parker s.n.* (K) ; Ambalavao Distr., Ambohimahasina Canton, Ambohitrampanefy village [S 21.56, E 47.11], *Cours 5002* (P) ; Andringitra massif, Ambodipaiso forest nr. Antsoabe, around Manak West [S 22.12 c, E 46.52 c], *Cours 2330* (P) ; around Ranotsara, nr. Ihosy [S 22.47, E 46.38], *Bosser 18563* (P × 2) ; Pic St. Louis, around Fort Dauphin [S 25.02, E 46.58], *Humbert 5900 ter* (P). — No locality given (or only "Central Madagascar" or "Central Plateau") : *Baron 2945, 3534* (both K, P), *3204* (BM, K, P), *3657, 3841* (both P) ; *Hodgkin & Stansfield 288* (K) ; *Homolle 2, 174, 802, 2659, CC, s.n.* (all P), *G3* (P ; mixed with *D. andribensis*). — Not traced : "top of Ifody mountain", *Baron 1375* (P) ; Analamihilana forest, *Cours 2010* (P) ; Imerina : Ifanangvávana hill, *Hildebrandt 3809* (BM, K, P, W, WU).

11. *Danais aurantiaca* Homolle. — Fig. 8, D.

Not. Syst. (Paris) 5 : 280 (1936) ; BOITEAU, Bull. Acad. Malg. 24 : 11 (1941).

TYPE : *Perrier de la Bâthie 6895*, Madagascar, Analamazaotra (holo-, P!).

Woody lianas or climbing shrubs with branched stems to ca. 8 m long, mostly glabrous, occasionally pubescent or puberulous when young but soon glabrescent. Leaves decussate (very rarely some leaves in whorls of 3) ; leaf-blades coriaceous, (ob)ovate, elliptic to ± lanceolate, 30-110 × (10-)15-40(-55) mm, acute to shortly acuminate at the apex, cuneate at the base, glabrous on both surfaces or a little hairy below, the reticulate venation pattern usually conspicuous on the upper surface ; petioles 6-12(-20) mm long, glabrous to hairy ; stipules triangular, to ca. 2 mm long, mostly glabrous.

Inflorescences predominantly in the axils of foliage leaves, flowers several to many in rather congested to somewhat elongated clusters ; sometimes also a terminal inflorescence present ; peduncles and pedicels mostly glabrous, seldom pubescent, the former 7-22 mm long, the latter often very short (1 mm or less) ; ultimate bracts ± linear, often < 1 mm long. Flowers 5-merous, heterodistylous ; calyx lobes narrowly triangular, mostly < 1 mm long, erect to ± spreading, mostly glabrous. Corolla tube greenish-white, lobes orange ; tube (4-)5-9 mm long, narrowly funnel-shaped to ± cylindrical, ca. 0.5 mm wide at the base, ca. 0.7 mm wide above in short-styled and ca. 1.2-1.4 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers ; lobes linear-lanceolate, (1.5-)2-4 × 1 mm, ± spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. 3 mm in short-styled flowers ; anthers ca. 1.5 mm long. Style plus stigmas 8-9 mm long in long-styled flowers,

shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2 mm long. Ovary subglobose, ca. 1 mm long, glabrous or pubescent.

Capsule very woody, subglobose, ca. 4-8 mm in diam., glabrous; the bases of adjacent fruits (plus the pedicels) typically fused. Seeds dark brown, 1.7-2 mm in diam., with an irregularly lacerate circumferential wing. — B & P - Fig. 10, D.

Pollen : 3(-4)-colporate; average diam. : 10-14  $\mu\text{m}$ .

ECOLOGY AND PHENOLOGY : Mostly in eastern lowland rain forest ("forêt orientale", occasionally also in forests of higher altitudes (Central Plateau); in primary forest but also in disturbed, secondary sites such as in clearings or in savoka vegetation. — Alt. : 0-1200 m. — Flowers September-October, January, June; fruits September-November, January, April.

DISTRIBUTION (Fig. 7, D) : Endemic to East Madagascar.

CRITICAL REMARKS : *D. aurantiaca* has rather frequently been confused with *D. pubescens* with which it indeed shows agreement in certain characters (inflorescence position, corollas, thick-walled capsules, and fruits and seeds of often overlapping sizes). A good distinction character to *D. pubescens*, however, is the partial fusion of adjacent fruits (the pedicels, which may become quite woody and flattened, are normally included in this fusion; cf. BUCHNER & PUFF, 1993 : Fig. 10, D). Another characteristic feature of *D. aurantiaca* is the conspicuous reticulate venation pattern of the upper leaf blade surface (Fig. 8, D).

MATERIAL EXAMINED. — MADAGASCAR : Between Mandritsara [S 15.50, E 48.49] and Andilamena [S 17.01, E 48.35], *Perrier de la Bâthie* 15474 (P); Sainte-Marie [S 16.50, E 49.55], *Boivin s.n.* (P); Imerimandroso Canton [S 17.26, E 48.35], *Réserves Naturelles Mad RN 10891* (P); Fenerive Distr., Sahatavy [S 17.27, E 49.00], *Réserves Naturelles Mad RN 7825* (P); from Manakambahiny [Est] to Nonokambo [S 17.46, E 48.42 c], *Cours* 2358 (P); from Fotsimavo to Betampona Nat. Res., ca. 50 km NW Tamatave [S 17.54, E 49.13], *Gentry* 11310 (MO); 11 km E of Beforona [S 18.55 c, E 48.45 c], *Gentry* 11271 (K, MO); around Andasibe (= Perinet) [S 18.56, E 48.25], *Barnett & Dorr* 143, 147 (both MO); N of Tamatave rd., on trail to Analamazoatra, *Lowry & Schatz* 4268 (K  $\times$  2, MO); 1 km W Perinet, Route Nationale 2, *Lorence* 2021 (K, MO); Analamazoatra, *Perrier de la Bâthie* 6895, 6935 (both P); Moramanga - Anosibe rd., km 29 [S 19.08 c, E 48.15 c], *Bosser* 6728 (P); Anosibe, Moramanga Distr. [S 19.26, E 48.13], *Decary* 18290 (P); Analatery - Ambositra [S 20.31, E 47.15], *Razafindrambao* 174 (P; mixed with *D. cernua*); between Mahanoro [S 19.54, E 48.48] and Mananjary [S 21.15, E 48.10], *Perrier de la Bâthie* 14248 (P); Mananjary, *Perrier de la Bâthie* 3934 (P). — No locality given : *Homolle* 154, 1730, 1951, 2358 (all P).

## 12. *Danais magna* Puff & Buchner, *sp. nov.* — Fig. 9.

*D. pubescens affinis sed foliis majoribus, petiolis longioribus et floribus brevioribus differt.*

TYPE : *Schatz & Carlson* 2914, Madagascar, Nosy Mangabe, 2-19.I.1990 (holo-, MO!; iso-, K!).

Woody lianas with branched stems to ca. 25 m long, younger parts finely pubescent or puberulous. Leaves decussate; leaf-blades coriaceous, (ob)ovate to ovate-lanceolate, 70-110  $\times$  (25-)35-60 mm, mostly with an indistinct, blunt tip at the apex, rounded to  $\pm$  cuneate at the base,  $\pm$  glabrous above and entire lower surface finely pubescent; petioles (10-)15-30 mm long, finely pubescent; stipules broadly triangular, to ca. 5 mm long, hairy.



Fig. 9. — Holotype of *Danais magna* (Schatz & Carlson 2914, MO). — Scale bar : 10 cm.

Inflorescences predominantly in the axils of foliage leaves, flowers  $\pm$  many in rather congested, subsessile to shortly pedunculate clusters ca. 30 mm in diam.; sometimes also a terminal inflorescence present; peduncles and pedicels hairy, the former to 7 mm long, the latter  $\pm$  0-2 mm; ultimate bracts  $\pm$  linear-lanceolate, mostly  $<$  1 mm long. Flowers 5-merous, heterodistylous; calyx lobes narrowly lanceolate, usually  $<$  1 mm long,  $\pm$  erect, hairy. Corolla tube greenish to whitish, lobes orange; tube 4-6 mm long, narrowly funnel-shaped to  $\pm$  cylindrical, ca. 0.5-0.8 mm wide at the base, ca. 0.8 mm wide above in short-styled and ca. 1.2 mm in long-styled flowers, outside glabrous,  $\pm$  densely pilose in the throat, particularly in long-styled flowers; lobes oblong,  $2.5-3 \times 0.8-1$  mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. 5-6 mm in short-styled flowers; anthers ca. 1-1.5 mm long. Style plus stigmas 6-9 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2-3 mm long. Ovary subglobose, ca. 1 mm long, hairy.

Mature fruits and seeds unknown.

ECOLOGY AND PHENOLOGY : In eastern lowland rain forest ("forêt orientale"); plants climbing 20 to 25 m into the canopy. — Alt. : 0-330 m. — Flowers January-March; mature fruits unknown.

DISTRIBUTION (Fig. 7, E) : Endemic to Northeast Madagascar.

CRITICAL REMARKS : In spite of the absence of mature fruits and of seeds, there seems to be little doubt that *D. magna* is to be considered a member of the "*D. pubescens* group". It appears to be closest to *D. pubescens*, from which it differs in its larger, rather long-petiolate leaves with a somewhat different kind of indumentum, in its often shorter corolla tubes and its mostly less distinctly pedunculate inflorescences.

MATERIAL EXAMINED. — MADAGASCAR : Sambava [S 14.16, E 50.10], *Réserves Naturelles Mad RN 8823* (P); Marosaina, Antalaha [S 15.25, E 50.22], *Réserves Naturelles Mad RN 7094* (P); Nosy Mangabe [S 15.30, E 49.46], *Schatz et al. 1843* (K, MO), *Schatz & Carlson 2914* (K, MO). — No locality given : *Belanger 107* (P).

### 13. *Danais capituliformis* Homolle

Not. Syst. (Paris) 5 : 282 (1936); BOITEAU, Bull. Acad. Malg. 24 : 8 (1941).  
— *Danais ambanjensis* LEROY, *nom. nud.* [on a note attached to the herbarium sheet *RN 7372* (P)].

TYPES : *Perrier de la Bâthie 15330*, Madagascar, Tsaratanana (lecto-, P!, selected here); *Perrier de la Bâthie 15133*, plateau de Mrangaka [HOMOLLE misread the locality as "Miangaky"] (syn-, P!).

Woody lianas, lengths of the stems unknown; at least the younger parts pubescent. Leaves decussate; leaf-blades thinly coriaceous to  $\pm$  membranous, elliptic to ovate,  $30-100 \times 10-60$  mm, acute to indistinctly acuminate at the apex, cuneate to  $\pm$  rounded at the base, rather densely pubescent below (especially on the veins), indumentum less dense and shorter above,

venation raised and prominent on the lower surface; petioles 3-17 mm long, pubescent; stipules triangular to  $\pm$  deltoid below, apically with a median, often  $\pm$  curved setose appendage, ca. 2-5 mm long, often pubescent.

Inflorescences long-stalked, solitary, several- to  $\pm$  many-flowered head-like clusters in the axils of foliage leaves, or head-like flower clusters terminal on short, branched lateral shoots; peduncles ca. 5-45 mm long, hairy, pedicels  $\pm$  0. Flowers 5-merous, heterodistylous; calyx lobes lanceolate to  $\pm$  spathuliform, ca. 1.5-3.5 mm long, hairy. Corolla dark red; tube ca. 12 mm long,  $\pm$  cylindrical, ca. 0.6-0.7 mm wide at the base, ca. 0.8-0.9 mm wide above in short-styled flowers, outside hairy; lobes lanceolate, 3.5-4  $\times$  0.6-0.8 mm,  $\pm$  spreading, a little hairy outside. Stamens exerted for ca. 2.5-3 mm in short-styled flowers; anthers ca. 1.5 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers unknown). Ovary subglobose, ca. 1 mm long, pubescent.

Capsule subglobose, ca. 4-4.7 mm in diam., hairy to glabrescent. Seeds<sup>1</sup> dark brown, ca. 0.9-1.2 mm long or in diam., with an irregularly lacerate, often  $\pm$  elongated and asymmetrical circumferential wing.

ECOLOGY AND PHENOLOGY : In scrub (no other data available). — Alt. : ?-1600-2000 m. — Flowers December-January; fruits ? October.

DISTRIBUTION (Fig. 7, C) : Endemic to Northern Madagascar.

CRITICAL REMARKS : The type specimens are somewhat heterogeneous : *Perrier de la Bâthie* 15133 not only has smaller leaves with shorter petioles but also more extensive, branched inflorescences and smaller and narrower calyx lobes than *Perrier de la Bâthie* 15330. The only other collection known, RN 7372, more closely resembles the latter.

The species somewhat approaches the genus *Payera* in having hairy corollas and head-like inflorescences (but a distinct involucre, as is characteristic for species of that genus, is absent; cf. BUCHNER & PUFF, 1993). The lianescent habit and the axillary inflorescences of *D. capituliformis*, on the other hand, are characters which are never found in *Payera*. — *D. capituliformis* is suspected to be distantly related to *D. pubescens*, some forms of which also have hairy corollas.

MATERIAL EXAMINED. — MADAGASCAR : Ambanja [S 13.41, E 48.27], *Réserves Naturelles Mad* RN 7372 (P  $\times$  2); Mt. Tsaratanana [S 14.00 c, E 49.00 c], *Perrier de la Bâthie* 15330 (P); Mrangaka plateau [Ankaizina, NE of Bealanana] [S 14.25 c, E 48.50 c], *Perrier de la Bâthie* 15133 (P).

Species 14-15 appear to be allied. The species pair is characterized by stipules unusual in the genus (bi- or multifimbriate, respectively), typically hairy stems and leaves, relatively long corolla tubes (cf. Fig. 3) and long calyx lobes.

1. From not yet dehisced capsules that were forced open; the seeds are possibly still immature (seed wings not yet fully developed).

14. *Danais andribensis* Homolle. — Fig. 2, C.

Not. Syst. (Paris) 5 : 279 (1936); BOITEAU, Bull. Acad. Malg. 24 : 12 (1941).

TYPE : *Perrier de la Bâthie* 3632, Madagascar, mountain summit around Andriba (holo-, P!).

Small woody lianas with stems ca. 3 (-?) m long, finely pubescent or puberulous when young but soon glabrescent. Leaves decussate; leaf-blades thinly coriaceous to  $\pm$  membranous, ovate or ovate-elliptic, 35-70  $\times$  20-40 mm, shortly acuminate at the apex,  $\pm$  cordate to rounded at the base, scabrous above, finely pubescent below, the venation conspicuous especially on the lower surface; petioles 2-7(-10) mm long, pubescent; stipules bifid, with a basal triangular part (0.5-1.5 mm long) and two  $\pm$  filiform, often curved appendages to ca. 2-3(-7) mm long, finely pubescent.

Inflorescences terminal and in the axils of foliage leaves, flowers several in rather congested clusters; peduncles and pedicels pubescent, the former to 10 mm long, the latter usually shorter, often ca. 3-7 mm long; ultimate bracts linear, to 2 mm long, pubescent. Flowers 5-merous, heterodistylous; calyx lobes linear to  $\pm$  filiform, (2-)3-8 mm long, erect at first, later spreading to reflexed, hairy. Corolla yellowish-brown to dark brown (lobes?); tube 12-15(-18) mm long, narrowly funnel-shaped to  $\pm$  cylindrical, ca. 0.5 mm wide at the base, ca. 1.5 mm wide above in long-styled flowers, glabrous outside, hairy in the throat; lobes oblong, 4-5  $\times$  1 mm, glabrous. Stamens included in long-styled flowers (short-styled flowers unknown). Style plus stigmas 15-20 mm long in long-styled flowers, presumably shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2 mm long. Ovary subglobose, ca. 1.5 mm long, pubescent.

Capsule rather thin-walled, subglobose, ca. 4-8 mm in diam., glabrescent to glabrous, the valves  $\pm$  sulcate. Seeds dark brown, 1.5-2 mm in diam., with a broad irregularly lacerate circumferential wing.

ECOLOGY AND PHENOLOGY : At the edge of forest (remnants). — Alt. : ?-600-? m. — Flowers April-May; fruits June, August.

DISTRIBUTION (Fig. 10, A) : Endemic to Madagascar. See also Critical remarks, below.

CRITICAL REMARKS : The distribution of this species is conspicuously disjunct (cf. Fig. 10, A). Although "northern" and "southern" collections do differ in some features (notably in the calyx lobe size, shape and indumentum: longer, narrower and less hairy in the former than in the latter), the differences are believed to be too insignificant to warrant a taxonomic recognition as, for example, geographical subspecies. It is, in our opinion, not to be discounted altogether that the disjunct distribution range reflects an unnatural situation and finds its explanation in the heavy destruction of the natural vegetation that has taken place on Madagascar's Central Plateau in the past century.

*D. andribensis* is the only species in the genus which has stipules that apically bear two distinct and often relatively long appendages (Fig. 2, C). — As regards the occasional occurrence of indistinctly bifid stipules see also *D. cernua* (Critical remarks).



Fig. 10. — Distribution of *Danais* species. — A, *D. andribensis*. — B, *D. vestita*. — C, *D. tsaratananensis*. — D, *D. nigra* [\* *D. perrieri*; see text]. — E, *D. dauphinensis*. — F, *D. terminalis*. — In A-E the dotted line marks the border between the East and West Malagasy Region, in F the western border of the Eastern Domain of the East Malagasy Region.



MATERIAL EXAMINED. — MADAGASCAR : Sahamaloto, W of Lac Alaotra [S 17.25, E 48.19], *Bosser* 8127 (P); mountain summit around Andriba [S 17.36, E 46.55], *Perrier de la Bâthie* 3632 (P); Anketsihetsy, Begogo Canton, Poste Iakora [S 23.24, E 46.45], *Cours* 5203 (P); around Ampandrandava (between Bekily and Tsivory) [S 24.05, E 45.42], *Seyrig* 647 [? = *Herb. Jard. Bot. Tana* 6279]<sup>1</sup> (both P). — No locality given : *Homolle* 2007 (P), *G3* (P; mixed with *D. pubescens*).

15. *Danais vestita* Baker. — Fig. 2, D; 5, C.

J. Linn. Soc. (Bot.) 21 : 408 (1885); BOITEAU, Bull. Acad. Malg. 24 : 10 (1941).

— *Rondeletia ferruginea* A. RICH., *nom. nud.* [e.g. Madagascar, E coast, *Chapelier s.n.* (P!); without locality, no collector, no date, *Herb. A. Richard* (P!)]

TYPE : *Baron* 2329, Madagascar, “Central Madagascar” (holo-, BM!; iso-, K!, P!).

Climbing shrubs with branched stems to ca. 5 m long, most parts densely covered with typically rusty or golden brown long hairs, rarely  $\pm$  glabrescent. Leaves decussate (very rarely some leaves in whorls of 3); leaf-blades thinly coriaceous to  $\pm$  membranous, ovate or ovate-elliptic, 45-110  $\times$  25-50(-55) mm, shortly to long acuminate at the apex,  $\pm$  cordate to rounded at the base, densely hairy below, hairs fewer and shorter above, the venation conspicuous especially on the lower surface; petioles 3-10 mm long, pubescent; stipules pluri- to multifimbriate, the filiform appendages 4-10(-13) mm long, often  $\pm$  curved, hairy.

Inflorescences in the axils of foliage leaves, not uncommonly also terminal and axillary, flowers several to many in pedunculate rather loose to  $\pm$  congested clusters; peduncles and pedicels pubescent, the former to 10 mm long; pedicels short at first ( $\pm$  0-3 mm long), often elongated and up to ca. 15 mm long in fruit; ultimate bracts small to minute, densely hairy. Flowers 5-merous, heterodistylous; calyx lobes narrowly linear-lanceolate to  $\pm$  filiform, 3-6(-10) mm long (usually somewhat longer after anthesis than before), erect at first, later spreading and often variously curved, hairy. Corolla tube greenish(-pink), lobes pink to salmon red; tube (10-)13-17(-22) mm long, narrowly funnel-shaped, ca. 0.5 mm wide at the base, ca. 1.2 mm wide above in short-styled and ca. 1.4 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes linear-lanceolate, 3.5-4  $\times$  0.8 mm, glabrous. Stamens included in long-styled flowers but exserted for ca. 4-5 mm in short-styled flowers; anthers ca. 1-1.5 mm long. Style plus stigmas 16-21 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exserted, filiform stigma lobes of long-styled flowers ca. 3.5-5 mm long. Ovary subglobose, ca. 1.5-2 mm long, usually densely pubescent.

Capsule rather thin-walled, subglobose but laterally indistinctly to distinctly compressed, 6-11 mm in diam., or sometimes somewhat wider than high, 6-11  $\times$  6-9 mm, hairy to glabrescent, the valves sulcate. Seeds brown, 1.8-3 mm in diam., with a broad, irregular, somewhat eccentric circumferential wing, indistinctly bipartite at the base.

ECOLOGY AND PHENOLOGY : At the edge of evergreen forest, in scrub. — Alt. : 100-1200-? m. — Flowers October, March, May; fruits September-October.

1. The two sheets, bearing different labels (but giving the same collecting locality), seem to be identical. On each of the two sheets two different sets of collections of *D. andribensis* are mounted. It is highly unlikely that the two specimens on each sheet are from the same locality. It rather seems that one is a “southern” and the other a “northern” collection (cf. Critical remarks).

DISTRIBUTION (Fig. 10, B) : Endemic to East Madagascar.

CRITICAL REMARKS : The species is unique within the genus in having multifimbriate stipules (Fig. 2, D). The latter, in combination with the conspicuous indumentum (all parts typically densely covered with long, usually rusty-brown hairs), makes it easy to recognize the species even in vegetative state.

The northernmost collection of *D. vestita* (Miller et al. 3326) is rather atypical. While agreeing with typical material, inter alia, in having multifimbriate stipules, it differs in having shoots with some ternately arranged leaves, somewhat fewer-flowered inflorescences and a less dense, not rusty-brown but whitish indumentum. It exhibits some similarity to the presumably closely allied *D. andribensis*.

MATERIAL EXAMINED. — MADAGASCAR : Antsiranana, N. of Mandena, between Mandena and Marojejy Res. [S 14.27, E 49.17], Miller et al. 3326 (K, ex MO) ; Ambodimanga to Antanambao [S 17.30 c, E 48.50 c], Cours 2785 (P) ; Tamatave Distr., Mangabe [S 17.44, E 49.13], Decary 16834 (P) ; R.N. I [Ambodiriana] [S 17.56, E 49.17], Réserves Naturelles Mad RN 3950 (P) ; Perinet (= Andasibe) [S 18.56, E 48.25], Bosser 2201 (P), d'Arcy 15299 (MO) ; Analamazaotra, Herb. Jard. Bot. Tana s.n. (P) ; Moramanga Distr., Anosibe [S 19.26, E 48.13], Decary 18269 (P). — Without precise locality ("Madagascar", "Central Madagascar", "East Coast") : anon. coll. s.n. (herb. Maire, herb. Cosson) (P) ; Baron 2329 (BM, K, P), 4003 (K), s.n. (P × 2) ; Bojer s.n. (BM) ; Chapelier s.n. (P) ; herb. Richard s.n. (P).

Species 16-22 are likely to be a rather heterogeneous group, held together by usually long corolla tubes and often large fruits and seeds (cf. Fig. 3 and 4). Within this group, some obviously allied subgroups are recognizable (see the Critical remarks section of the respective species).

## 16. *Danais tsaratananensis* Homolle

Not. Syst. (Paris) 5 : 287 (1936) ; BOITEAU, Bull. Acad. Malg. 24 : 13 (1941).  
— *Danais humbertii* CAVACO, Adansonia, sér. 2, 5 : 439 & pl. 1, 16-20 (1965). Type : Humbert 23818, Madagascar, Marojejy massif, W of upper Manantenina, tributary of Lokoho (holo-, P!).

TYPE : Perrier de la Bâthie 16189, Madagascar, Mt. Tsaratanana (holo-, P!).

Woody lianas or climbing shrubs with branched glabrous stems ca. 2 (-?) m long. Leaves decussate ; leaf-blades coriaceous, ovate-lanceolate to lanceolate, 40-75 × (10-)20-35 mm, long acuminate at the apex, ± cordate or rounded at the base, glabrous, the veins raised and prominent above and below ; petioles 8-15 mm long, glabrous ; stipules broad at the base, with a median tooth-like appendage, to ca. 1.8 mm long, glabrous.

Inflorescences terminal and axillary, flowers several to many in rather loose, pedunculate clusters ; peduncles and pedicels glabrous, the former to 10 mm long, the latter ca. 2-3 mm ; ultimate bracts minute, < 1 mm long. Flowers 5-merous, heterodistylous ; calyx lobes narrowly lanceolate, to 1 mm long, erect, glabrous. Corolla tube olive-yellow, lobes coral or wine red ; tube 8-10 mm long, ± cylindrical, ca. 0.8 mm wide at the base, ca. 1 mm wide above

in short-styled and ca. 1.3 mm in long-styled flowers, glabrous outside, pilose inside; base of tube with splits; lobes lanceolate,  $3-4 \times 1$  mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exerted up to ca. 4 mm in short-styled flowers; anthers ca. 1.5-2 mm long. Style plus stigmas 10-12 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2-3 mm long. Ovary subglobose, ca. 1 mm long, glabrous.

Capsule subglobose, rather thin-walled, 7-10 mm in diam., glabrous, sometimes indistinctly ribbed. Seeds dark brown, 1-2 mm in diam., with an irregularly lacerate circumferential wing.

Pollen : 3(-4)-colporate; average diam. : 14-20  $\mu$ m.

ECOLOGY AND PHENOLOGY : In or at the edge of forest, including in high altitude forest rich in lichens ("sylve à Lichens") over gneiss and quartzite (Marojejy summit); also in "bush" (scrub forest). — Alt. : 1000-2100 m. — Flowers March-April; fruits March-May.

DISTRIBUTION (Fig. 10, C) : Endemic to North Madagascar; confined to the Tsaratanana and Marojejy massif.

CRITICAL REMARKS : The types of *D. tsaratananensis* and *D. humbertii* differ in leaf shape (the latter has broader blades which are  $\pm$  cordate at their base), but other collections are intermediate in this respect. As there are no significant disagreements in other character states, the two are best united.

As already noted under *D. humblotii*, there may be a distant relationship between that species and *D. tsaratananensis*.

MATERIAL EXAMINED. — MADAGASCAR : Mt. Tsaratanana [S 14.00 c, E 49.00 c], *Perrier de la Bâthie* 16189 (P); Bealanana Distr., Mangindrano Canton, R.N. IV [S 14.17, E 48.58], *Réserves Naturelles Mad RN 5217* (P); Marojejy massif [S 14.27 c, E 49.45], summit, *Cours 3509* (P); W of upper Manantenina, tributary of Lokoho, *Humbert 23818* (P); Lohoko valley, Mt. Beondroka, N of Maroambihy [S 14.30 c, E 49.52], *Humbert 23481* (P).

## 17. *Danais nigra* Homolle

Not. Syst. (Paris) 5 : 286 (1936); BOITEAU, Bull. Acad. Malg. 24 : 7 (1941).

TYPES : *Perrier de la Bâthie* 16277, Madagascar, lower Sambirano [River] (lecto-, P!, selected here); *Perrier de la Bâthie* 3830, Analalava prov., around Loza [River] (syn-, P!).

Woody lianas or climbing shrubs with branched glabrous stems to ca. 8 m long. Leaves decussate; leaf-blades coriaceous, ovate to elliptic,  $50-120 \times (15-20-55)$  mm, acute to shortly acuminate at the apex, cuneate to  $\pm$  rounded at the base, glabrous; petioles  $(5-8-15(-20))$  mm long, glabrous; stipules triangular, to ca. 1 mm long, glabrous.

Inflorescences terminal, rather lax,  $\pm$  rounded, to ca. 10 cm in diam.,  $\pm$  many-flowered, glabrous; peduncles 10-50 mm long; pedicels  $(5-7-12)$  mm long; ultimate bracts  $\pm$  filiform, to 2 mm long. Flowers 5-merous, heterodistylous; calyx lobes narrowly triangular to  $\pm$  filiform,  $(0.5-1-2)$  mm long, spreading to  $\pm$  recurved, glabrous. Corolla black, blackish-brown,

but  
2-3 mm or  
material det by them

lavender, light purple or golden olive (inner surface of lobes also yellow-orange); tube (11-) 13-20 mm long,  $\pm$  cylindrical, < 1 mm wide at the base, ca. 1 mm wide above in short-styled and to ca. 1.8 mm in long-styled flowers; lobes linear-lanceolate, (4-)6-9  $\times$  0.7-0.9 mm, spreading to  $\pm$  recurved, glabrous. Stamens included in long-styled flowers but exerted for 4-8 mm in short-styled flowers; anthers ca. 1.5-2 mm long. Style plus stigmas 17-25 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers 2-3 mm long. Ovary subglobose, ca. 1-1.5 mm long, glabrous.

Mature fruits and seeds unknown. — B & P - Fig. 3, H.

Pollen : 4(-5)-colporate; average diam. : 22-26  $\mu$ m.

ECOLOGY AND PHENOLOGY : In eastern lowland rain forest ("forêt orientale"); in forest over sandstone (Sambirano), in dry bush; gneiss hills (Loza R.). — Alt. : 200-550 m. — Flowers October-November, March-April, June; mature fruits unknown.

DISTRIBUTION (Fig. 10, D) : Endemic to North Madagascar.

CRITICAL REMARKS : The species apparently occurs in rather diverse environments, ranging from wet forest habitats to dry bush, e.g. *Decary 2136*; the latter collection looks rather depauperate, having rather small, elliptic to lanceolate leaves hardly more than 60 mm long and 20 mm wide.

The relationships of *D. nigra* remain somewhat obscure because mature fruits are unknown. It is perhaps allied to other *Danais* taxa with long corolla tubes and coriaceous leaves, e.g. the species pair *D. volubilis*-*D. coronata* which, however, differs in having essentially axillary inflorescences. *D. terminalis* has basically similar (although fewer-flowered, more reduced) terminal inflorescences, but open flowers of that species are unknown.

MATERIAL EXAMINED. — MADAGASCAR : Lower Sambirano [S 13.50 c, H 48.30 c], *Perrier de la Bâthie 16277* (P); Maromandia [S 14.10, E 48.06], *Decary 2136* (P); Analalava prov., around Loza [River] [S 14.35 c, E 47.45 c], *Perrier de la Bâthie, 3830* (P); Masoala peninsula, NW coast, ESE of Maroantsetra, H and S of Hiaraka village [S 15.30 c, E. 49.54 c], *Lowry et al. 4061, 4100* (both K, MO); ca. 3 km NE of Antalavia, along Antalavia R. [S 15.47, E 50.02], *Schatz et al. 2823* (K, MO).

Tentatively included in *D. nigra* is the following species :

### *Danais perrieri* Homolle

Not. Syst. (Paris) 5 : 286 (1936); BOITEAU, Bull. Acad. Malg. 24 : 9 (1941). Type : *Perrier de la Bâthie 14752*, Madagascar, Mt. Andriantantely [S 18.42, E 48.48], N of Anivorano (holo-, P!).

The species, only known from the type, exhibits some morphological differences to *D. nigra*. Its leaves not only have shorter petioles (ca. 5 mm) but are also less distinctly coriaceous than in *D. nigra*; the calyx lobes are also shorter, not more than 0.5 mm long. In other character states, notably the conspicuous lax inflorescences and the long-tubed flowers with their long corolla lobes, there is agreement to *D. nigra*. Although the type specimen was

collected in an area that is clearly outside the distribution range of *D. nigra* (i.e, from much further South ; cf. Fig. 10, *D*) the differences do not seem to be substantial enough to uphold *D. perrieri* as a separate species.

### 18. *Danais dauphinensis* Cavaco

Adansonia, sér. 2, 5 : 439 & pl. 1 (11-15) (1965).

TYPE : *Humbert 20350*, Madagascar, Manantantely forest, nr. Fort Dauphin (holo-, P!).

Climbing shrub, stems ca. 1 (-?) m long, glabrous. Leaves decussate ; leaf-blades coriaceous, elliptic-lanceolate, 45-95 × 10-35 mm, acute at the apex, cuneate at the base, glabrous ; petioles 4-15 mm long, glabrous ; stipules triangular to ± deltoid, to ca. 1-1.5 mm long, glabrous.

Inflorescences terminal and also axillary, rather lax, ± rounded, to ca. 5 cm in diam., several-flowered, glabrous ; peduncles 7-15 mm long ; pedicels (2-)4-7 mm long ; ultimate bracts ± filiform, < 1 mm long. Flowers 5-merous, heterodistylous ; calyx lobes ± filiform, < 1 mm long, erect to ± spreading, glabrous. Corolla whitish to olive green ; tube (8-)9-17 mm long, ± cylindrical, ca. 0.5 mm wide at the base, ca. 1.3 mm wide above in short-styled flowers ; lobes linear-lanceolate, 4-6 × 1 mm, spreading, glabrous. Stamens exerted for ca. 4 mm in short-styled flowers ; anthers ca. 2 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers unknown). Ovary subglobose, ca. 1 mm long, glabrous.

Capsule rather thin-walled, subglobose, ca. 4.5-7 mm in diam., glabrous. Seeds dark brown to blackish, ca. 2 mm in diam., with an irregularly lacerate circumferential wing.

ECOLOGY AND PHENOLOGY : In forest over lateritic clay and granite, also in the transition zone between xerophilous bush and sclerophyllous forest of the Western slopes [forêt basse sclérophylle"]. — Alt. : (?50-)300-900 m. — Flowers and fruits January-March.

DISTRIBUTION (Fig. 10, *E*) : Endemic to Southeast Madagascar.

CRITICAL REMARKS : Some of the species' character states remind of the North Madagascan *D. nigra* : leaf texture, leaf-blade shapes and sizes and also the corollas are similar. There are, however, differences in the inflorescences (terminal *and* axillary, not as extensive as in *D. nigra*). It remains to be seen whether there are also similarities in the fruits (at present, the fruits of *D. nigra* are unknown).

MATERIAL EXAMINED. — MADAGASCAR : Mts. between Andohahela and Elakelaka, Mt. Apiky below Mahamavo [S 24.45, E 46.43], *Humbert 13814* (P) ; Manantantely forest nr. Ft. Dauphin [S 25.02, E 47.00], *Humbert 20350* (P).

19. **Danais terminalis** Boivin ex Drake

Bull. Soc. Bot. France 45 : 350 (1898, publ. 1899); BOITEAU, Bull. Acad. Malg. 24 : 11 (1941).

TYPE : *Boivin 1773*, Madagascar, Sainte-Marie (holo-, P!; iso-, W!).

Climbing shrub, length of stems unknown, glabrous. Leaves decussate; leaf-blades (thinly) coriaceous, 40-60 × 25-30 mm, shortly acuminate at the apex, cuneate at the base, glabrous; petioles 4-7 mm long, glabrous; stipules triangular to ± deltoid, to ca. 1 mm long, glabrous.

Inflorescences 7- to 1-flowered, terminal on long shoots and sometimes also on short lateral branches, occasionally also axillary, elongated (to 10 cm long) and very lax, glabrous; inflorescence main axis with 3-1 pairs of pedicellate flowers, or only with a solitary terminal flower; pedicels 5-25(-30) mm long, often with two minute bracts (0.5 mm long) around the middle. Open flowers unknown; calyx lobes of young buds narrowly triangular, ca. 0.5 mm long.

Capsule rather thick-walled, subglobose, ca. 8-12 mm in diam., glabrous, the valves indistinctly sulcate. Seeds dark brown, ca. 2.5-4 mm in diam., with a broad irregularly lacerate, sometimes ± elongated circumferential wing. — B & P - Fig. 3, I.

ECOLOGY AND PHENOLOGY : In eastern lowland rain forest ("forêt orientale"). — Alt. : 0-100 m. — Fruits September (open flowers unknown).

DISTRIBUTION (Fig. 10, F) : Endemic to East Madagascar (eastern Domain).

CRITICAL REMARKS : The species, although incompletely known (open flowers are lacking), is well and easily distinguished by its characteristic inflorescence (cf. BUCHNER & PUFF, 1993 : Fig. 3, I).

On account of its relatively large fruits and seeds, a loose alliance to the species pair *D. coronata*-*D. volubilis* may be presumed. The latter, however, has essentially axillary inflorescences and large, conspicuous calyx lobes and, moreover, is characterized by having tough, thickly coriaceous leaves.

MATERIAL EXAMINED. — MADAGASCAR : Sainte-Marie [S 16.50, E 49.55], *Boivin 1773* (P, W); Vatomaniry [S 19.20, E 48.59], *Perrier de la Bâthie 14145* (P). — No locality given, *Lastelle s.n.* (P).

20. **Danais coronata** (Pers.) Steud.

Nom. ed. 1 : 263 (1821).

— *Danais fragrans* (LAM.) PERS. var. *coronata* PERS., Syn. Ench. 1 : 198 (1805); POIR., Encycl. Méth., Suppl. 2 : 450 (1812).

— *Danais littoralis* HOMOLLE, Not. Syst. (Paris) 5 : 285 (1936); BOITEAU, Bull. Acad. Malg. 24 : 6 (1941). Types : *Decary 10850*, Madagascar, around Fort Dauphin, Vinanibé (lecto-, P!, selected here; isolecto-, BR!); *Humblot 76*, without locality (syn-, K!, P!); *Perrier de la Bâthie 6943*, lower Matitana[na R.] (syn-, P!); *Decary 10767*, Soanierana (syn-, P!).



Fig. 11. — Distribution of *Danais* species. — A, *D. coronata*. — B, *D. volubilis*. — C, *D. pauciflora*. — D, *D. fragrans* in Madagascar. — E, *D. cernua*. — F, *D. distinctinervia* (\*) and *D. hispida*. — In B-F the dotted line marks the border between the East and West Malagasy Region, in A the western border of the Eastern Domain of the East Malagasy Region.

— *Danais purpurea* HOMOLLE, Not. Syst. (Paris) 5 : 287 (1936) ; BOITEAU, Bull. Acad. Malg. 24 : 6 (1941).  
Types : *Perrier de la Bâthie* 3973, Madagascar, lower Matitana[na R.] (lecto-, P!, selected here) ;  
*Humbert* 5828, around Fort Dauphin, Manantantely forest (syn-, P × 2!).

TYPE : *Commerson s.n.*, Madagascar, without locality (holo-, P! ; iso-, BM!).

Woody lianas or climbing shrubs with branched stems to ca. 3(-?) m long, glabrous, seldom puberulous on youngest parts. Leaves in whorls of 3 (occasionally also decussate on some shoots) ; leaf-blades thick and coriaceous, obovate, ovate, elliptic to ± lanceolate, (30-)50-100(-150) × (10-)20-50(-80) mm, mucronate, rounded or ± emarginate at the apex, gradually narrowed to the base, glabrous, shiny above, dull below ; petioles 4-13(-20) mm long, glabrous ; stipules broadly triangular, < 1 mm long, glabrous.

Inflorescences typically in the axils of foliage leaves (rather uncommonly also a terminal inflorescence present), flowers ± few to several in stalked, rather loose clusters ; peduncles and pedicels mostly glabrous, seldom puberulous, the former to ca. 15 mm long, the latter often ca. 1-5 mm long ; ultimate bracts linear, < 1 mm long. Flowers 5-merous, heterodistylous ; calyx lobes triangular, ca. 0.5-1.2(-1.5) mm long, erect to ± spreading, mostly glabrous. Corolla blackish, purplish-black, dark greenish-purplish or (?) deep scarlet ; tube 12-20 mm long, ± cylindrical, ca. 0.5-0.9 mm wide at the base, ca. 1-1.5 mm wide above in short-styled and ca. 1.6-2 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers ; base of tube with splits ; lobes oblong, 3-5 × 1.4-1.8 mm, ± spreading, glabrous. Stamens included in long-styled flowers but exserted for ca. 2.5-3 mm in short-styled flowers ; anthers ca. 1.5-2 mm long. Style plus stigmas 16-20 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers ; the exserted, filiform stigma lobes of long-styled flowers ca. 2 mm long. Ovary subglobose, ca. 1 mm long, glabrous or, seldom, puberulous.

Capsule rather thick-walled, subglobose, ca. 8-15 mm in diam., glabrous, the valves sulcate. Seeds (grey-) brown, 4-6 mm in diam., with a broad, circular wing with ± irregular margins. — B & P - Fig. 3, *D*<sub>1</sub>-*D*<sub>3</sub> ; 11, *E*-*G*.

Pollen : 4(-5)-colporate ; average diam. : 20-22 μm.

ECOLOGY AND PHENOLOGY : In coastal forest over sand, coastal dune forest or scrub in coastal dunes ; in taller forest immediately inland of dune forest ; also in eastern lowland rain forest (" forêt orientale "). — Alt. : 0-60(-300?) m. — Flowers June-September ; fruits August, October, December-January.

DISTRIBUTION (Fig. 11, *A*) : Endemic to East Madagascar.

CRITICAL REMARKS : *D. coronata* is undoubtedly very close the following species, *D. volubilis* (see there for further comments).

As indicated by its original description as a variety of *D. fragrans*, *D. coronata* shows some superficial resemblance to the former, notably in the thick, coriaceous leaves and the axillary inflorescences. Its long corolla tubes and large fruits and seeds (cf. Fig. 3 and 4), however, seem to exclude a closer relationship to *D. fragrans*.

MATERIAL EXAMINED. — MADAGASCAR : Ambil-Lemaitso, 10 km E Brickaville [S 18.51, E 49.08], *Schatz & d'Arcy* 1475 (MO) ; Beforona [S 18.58, E 48.35], *Decary* 18689 (P) ; lower Matitana[na R.] [S



22.26, E 47.55], *Perrier de la Bâthie* 3973, 6943 (both P); Vangaindrano [S 23.21, E 47.36], *Decary* 3879 (P), *Geay* 6769 (P), *Lantz s.n.* (P); Eroaroa [Erara], border of R.N. XI [S 24.47, E 46.53], *Service Forestier Mad SF* 26059 (P); Fort Dauphin pref., Lakandava [S 24.58, E 46.58], *Dumetz* 1243 (MO); Soanierana [S 25.00, E 46.53], *Decary* 10767 (P); Vinanibé, *Decary* 10850 (BR, P); Manantantely forest, W of Fort Dauphin, *Boiteau* 3071 B (P), *Humbert* 5828 (P × 2). — No locality given : *Commerson s.n.* (BM, P); *Humblot* 76 (K, P).

21. **Danais volubilis** Baker. — Fig. 12, E.

- J. Linn. Soc. (Bot.) 20 : 161 (1883); BOITEAU, Bull. Acad. Malg. 24 : 5 (1941).  
— *Danais clematidea* DRAKE, Bull. Soc. Bot. France 45 : 347 (1898, publ. 1899); BOITEAU, Bull. Acad. Malg. 24 : 5 (1941). Type : *Lastelle s.n.*, Madagascar, without locality (holo-, P!).  
— *Alleizettea bracteata* DUBARD & DOP, J. Bot. (Morot), sér. 2, 3 : 6 & fig. III (1925). Type : *d'Alleizette I*, Madagascar, North Imerina, Betsitra par Anjozorobé (holo-, P!).  
— *Danais latisepala* HOMOLLE, Not. Syst. (Paris) 5 : 284 (1936); BOITEAU, Bull. Acad. Malg. 24 : 8 (1941). Type : *Perrier de la Bâthie* 14076, Madagascar, nr. Brickaville (holo-, P!; iso-, P!).  
— *Danais longiflora* HOMOLLE, Not. Syst. (Paris) 5 : 284 (1936); BOITEAU, Bull. Acad. Malg. 24 : 12 (1941). Type : *Perrier de la Bâthie* 3727, Madagascar, Analamahitso, upper Bemarivo basin (holo-, P!; iso-, P!).

TYPE : *Baron* 1372, Madagascar, [top of Ifody mountain] (holo-, BM!; iso-, K!, P!).

Woody lianas or climbing shrubs with branched stems to ca. 5 m long, glabrous. Leaves in whorls of 3 or 4 (occasionally also decussate on some shoots); leaf-blades thick and coriaceous, obovate, ovate, elliptic to  $\pm$  lanceolate, 40-85  $\times$  20-50 mm, shortly acuminate, acute or mucronate at the apex, (gradually) narrowed to the base, glabrous, shiny above, dull below; petioles 5-15 mm long, glabrous, seldom puberulous; stipules broadly triangular to  $\pm$  deltoid, 0.5-2 mm long, glabrous.

Inflorescences typically in the axils of foliage leaves (occasionally also terminal on short lateral branches), flowers several to  $\pm$  many in subsessile or shortly stalked, rather loose to  $\pm$  dense clusters; peduncles and pedicels mostly glabrous, seldom puberulous, the former to ca. 10 mm long (usually less), the latter often ca. 1-4 mm long; ultimate bracts linear to lanceolate, to 5(-7) mm long. Flowers 5-merous, heterodistylous; calyx lobes narrowly lanceolate to linear-lanceolate, ca. (2.5-)3-9  $\times$  0.6-2 mm, erect to  $\pm$  spreading, glabrous or with short hairs on both sides or on the margins. Corolla blackish, (dark) brown, dark violet or dark reddish-purplish; tube 14-22 mm long,  $\pm$  cylindrical, ca. 0.5-0.8 mm wide at the base, ca. 1-1.2 mm wide above in short-styled and ca. 1.3-1.9 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes oblong, 3-7.5  $\times$  1-1.5 mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. 2-3 mm in short-styled flowers; anthers ca. 1.5 mm long. Style plus stigmas 18-20 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 2 mm long. Ovary subglobose, ca. 1-1.5 mm long, glabrous or puberulous.

Capsule rather thick-walled, subglobose, ca. 9-15 mm in diam., glabrous, the valves  $\pm$  sulcate. Seeds light brown, 3-6 mm in diam., with a broad,  $\pm$  regular circular wing. — B & P - Fig. 4, B-C; 10, A-B.

Pollen : 4(-5)-colporate; average diam. : 22-26  $\mu$ m (B & P - Fig. 15, G-I).

ECOLOGY AND PHENOLOGY : In forest over gneiss ; at the edge of forest (remnants) or in scrub ; in “ dry forest of the western slopes [of the Central Plateau] ” ; in savoka vegetation. — Alt. : 0-1600 m. — Flowers August-October, April, June ; fruits August-October, April.

DISTRIBUTION (Fig. 11, B) : Endemic to Madagascar.

CRITICAL REMARKS : The long, dark-coloured corolla tubes, the large fruits and seeds (cf. Fig. 3 and 4), the essentially axillary inflorescences, and the thick and tough leaves mostly in whorls of 3(4) are characters which provide solid evidence for the close alliance between *D. volubilis* and *D. coronata*. The two species, nevertheless, are easily kept apart by their calyx lobes (long in the former, small and inconspicuous in the latter). Moreover, there is a clear difference in their ecology and, to some extent, also in their distribution ranges (compare Fig. 11, A and B).

*D. longiflora* and *D. latisepala*, both only known from the type collections, are included. The former is considered an oddity (inflorescences both terminal and axillary rather than almost invariably axillary as in “ typical ” *D. volubilis*) which does not deserve taxonomic recognition, particularly since it agrees in all other character states. *D. latisepala* has somewhat wider calyx lobes than “ typical ” *D. volubilis*, but other features which were originally thought to be differential characters (calyx lobe length, indumentum) have since also been found in *D. volubilis*.

*D. sulcata*, a species endemic to Mauritius, appears to be a close ally of the species pair *D. coronata*-*D. volubilis*. It agrees in having axillary inflorescences, much elongated calyx lobes as in *D. volubilis* and rather large fruits.

MATERIAL EXAMINED. — MADAGASCAR : Analamahitso, upper Bemarivo basin [S 16.30 c, E 48.15 c], *Perrier de la Bâthie* 3727 (P × 2) [type of *D. longiflora*] ; Lac Alaotra [S 17.50 c, E 48.25 c], *Herb. Jard. Bot. Tana* 3861 (P) ; Majunga rd., PK 130, along Manankazo R. [S 18.09, E 47.12], *Bosser* 7922 (P) ; Tampoketsa d'Ankazobe, Ambohitantely (Forest Reserve), W of PK 125, Tananarive - Majunga rd. [S 18.12, E 47.17], *Cremers* 1618 (BR), *Puff, Igersheim & Rajemisoa* 850808-1/1 (TAN, WU) ; *Decary* 14944 (P) ; “ route d'Anjozorobé ”, *Herb. Jard. Bot. Tana* 3468 (P) ; North Imerina, Betsitra par Anjozorobé [S 18.22, E 48.00 c], *d'Alleizette* 1 (P) ; Betsitra, *d'Alleizette* 1209 M (P) ; Ankazondandy [S 18.42, E 47.47], *Boiteau* 78 B (P) ; North Imerina, hills N of Ambohimanga, tow. Analahi [S 18.44, E 47.34], *d'Alleizette* s.n. (P) ; nr. Brickaville [S 18.49, E 49.04], *Perrier de la Bâthie* 14076 (P × 2) [type of *D. latisepala*] ; Mandraka [S 18.55, E 47.46], *d'Alleizette* s.n. (P) ; Analamazaotra [S 18.56, E 48.25], *Herb. Jard. Bot. Tana* 3771 (P) ; route Moramanga-Anosibe, km 15 [S 19.03 c, E 48.15 c], *Bosser* 6616, 6619 (both P) ; Horombe plateau, western slopes, tow. Ranohira [S 22.30 c, E 45.30 c], *Humbert* 11204 (P) ; Fort Dauphin Distr., Enaniliha Canton [S 24.40, E 46.52], *Réserves Naturelles Mad RN* 8390 (P) ; upper Mananara basin, between Imonty and Mahamavo, Tsilotsilo hill [S 24.49, E 46.42], *Leandri & Saboureau* 4301 (P). — Not traced : “ top of Ifody mountain (E of Imerina) ”, *Baron* 1372 (BM, K, P). — No locality given : *anon. coll. s.n.* (P) ; *Baron* 2532 (K × 2, P-fragm.), 5091 (K) ; *Homolle* 38, 604 (both P) ; *Lastelle* s.n. (P).

## 22. *Danais pauciflora* Baker. — Fig. 12, C-D.

J. Linn. Soc. (Bot.) 20 : 162 (1883) ; BOITEAU, Bull. Acad. Malg. 24 : 5 (1941).

TYPE : *Baron* 1298, Madagascar, [forests of the province of Imerina] (holo-, BM! ; iso-, K × 2!, P!).

Presumably climbing shrubs with much-branched glabrous stems to ca. 3 m long. Leaves decussate (very seldom some leaves also in whorls of 3) ; leaf-blades thinly coriaceous, elliptic

to  $\pm$  obovate, 25-50  $\times$  12-21 mm, acute at the apex, (gradually) narrowed to the base, glabrous; petioles 3-7 mm long, glabrous; stipules triangular, ca. 0.8-1.5 mm long, glabrous.

Inflorescences terminal on short lateral branches and occasionally also axillary, flowers  $\pm$  few to several in subsessile clusters; pedicels ca. 0.8-4 mm long, glabrous; ultimate bracts linear,  $<$  1 mm long. Flowers 5-merous, heterodistylous; calyx lobes triangular, ca. 0.3-0.5 mm,  $\pm$  erect to spreading, mostly glabrous. Corolla brown; tube 17-19 mm long,  $\pm$  cylindrical, ca. 0.4 mm wide at the base, ca. 0.8-1 mm wide above in short-styled flowers, glabrous outside; lobes oblong, ca. 3  $\times$  0.8 mm,  $\pm$  spreading, glabrous. Stamens exerted for ca. 3-3.5 mm in short-styled flowers; anthers ca. 1.5 mm long. Style plus stigmas shorter than the corolla tube in short-styled flowers (long-styled flowers not seen). Ovary subglobose, ca. 1 mm long, glabrous.

Capsule subglobose, ca. 6-13 mm in diam., glabrous. Seeds dark brown, 2.5-4 mm in diam., with a broad,  $\pm$  circular wing with rather irregular margins.

ECOLOGY AND PHENOLOGY : “premontane rain forest”; no further data available. — Alt. : ?-900-? m. — Flowers December; no data for fruits.

DISTRIBUTION (Fig. 11, C) : Endemic to Central Madagascar.

CRITICAL REMARKS : The species, described as a “shrub”, is probably more correctly a **climbing** shrub (see also comments under *D. breviflora*!). It is only known from the type and a recollection (the first flowering specimen) from 1989.

The long, dark-coloured corolla tubes (probably phalenophilous flowers!), the seed structure (Fig. 12, C-D) and the large fruits are good indications that the species is likely to be an ally of the pair *D. coronata*-*D. volubilis*, although it differs in having essentially terminal inflorescences.

MATERIAL EXAMINED. — MADAGASCAR : Andasibe [S 18.56, E 48.25], *Miller & Randrianasolo 4705* (K, ex MO). — Imprecise locality : Imerina Prov., *Baron 1298* (BM, K, P).

Species **23-26** (“*Danais fragrans* group”) form a presumably natural group characterized by essentially axillary inflorescences, short to moderately long, funnel-shaped corollas (cf. Fig. 3) and rather thin-walled capsules.

### 23. *Danais fragrans* (Lam.) Pers.

Syn. Pl. 1 : 198 (1805); GAERTN. f., Suppl. Carp. [Fruct. 3] : 83 & *tab. 195* (1806); POIR., Encycl. Méth., Suppl. 2 : 450 (1812) [LAM., Ill. [Hist. Nat.] p. 257 : *pl. 166, 2 a-m*]; DC., Prodr. 4 : 361 (1830); BOJER, Hort. Maurit. : 164 (1837); BAKER, Fl. Mauritius and Seychelles 1 : 137 (1877); CORDEMOY, Fl. Réunion : 501 (1895); DRAKE in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : *tab. 451* (1898), *tab. 451A,2* (1900); BOITEAU, Bull. Acad. Malg. 24 : 4 (1941); VERDCOURT, Fl. Mascareignes, Rubiacées : 41 & *pl. 10* (1989).

— *Paederia fragrans* COMMERS. ex LAM., Encycl. Méth. 2 : 260 (1786) [this volume also issued as : Dictionnaire [Encycl. Méth.] 2 : 260 (1790)].

- *Danais rotundifolia* POIR., Encycl. Méth., Suppl. 2 : 450 (1812); DC., Prodr. 4 : 361 (1830); BOJER, Hort. Maurit. : 164 (1837). Type : *Bory*, “ l’Ile-de-Bourbon ” [Réunion] (holo-, P!).
- *Danais laxiflora* DC., Prodr. 4 : 361 (1830); BOJER, Hort. Maurit. : 164 (1837). Type : “ in ins. Mauritii aut Borboniae [Réunion] ... v. s. comm. à Mus. reg. Par. ” (holo-, G).
- *Danais lyallii* BAKER, J. Linn. Soc. (Bot.) 22 : 481 (1887). Types : *Baron 3895*, Madagascar, without precise locality (lecto-, K!, selected here); *Baron 1479* (syn-, n.v.), *3894* (syn-, P!); *Lyall 122* (syn-, n.v.); *Hildebrandt 3004*, Nosy-bé (syn-, BM!, P!, W!).
- *Danais obovata* DRAKE, Bull. Soc. Bot. France 45 : 348 (1898, publ. 1899), in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : tab. 453 (1898). Types : *Boivin s.n.*, Madagascar, without locality (lecto-, P!, selected here); *Humblot 36* (syn-, P!, W!); *Humblot 397* (syn-, P!, W!).
- *Danais nodulosa* DRAKE, Bull. Soc. Bot. France 45 : 350 (1898, publ. 1899); BOITEAU, Bull. Acad. Malg. 24 : 13 (1941). Type : *du Petit-Thouars s.n.*, Mauritius (n.v.).

TYPE : *Commerson s.n.*, Mauritius [“ Ile de France ”] [holo-, P-LA ; iso-, P, BM!, B-Willdenow 5104 (2 sheets)!, WU-photos!].

Woody lianas or climbing shrubs with branched stems to 12 m long, glabrous or sometimes with short hairs when young, occasionally lenticellate ; stems and leaves sometimes foetid when crushed. Leaves decussate ; leaf-blades typically thick, coriaceous, sometimes thinly coriaceous (to  $\pm$  membranous), obovate, broadly oblanceolate, ovate to almost orbicular, (oblong-)elliptic or  $\pm$  lanceolate, (40-)50-120  $\times$  (20-)25-80 mm, shortly acuminate or acute at the apex, (gradually) narrowed to the base or sometimes base  $\pm$  rounded ; typically glabrous above and below, occasionally with short hairs on midrib below ; petioles 5-15 mm long, glabrous or occasionally with short hairs ; stipules triangular to deltoid, ca. 1-3(-4) mm long, glabrous or, uncommonly, with short hairs on the margins.

Inflorescences predominantly in the axils of foliage leaves, flowers several to  $\pm$  many in subsessile and rather congested clusters or in somewhat elongated inflorescences (to ca. 7 cm in fruit) ; occasionally also a terminal inflorescence present ; peduncles and pedicels glabrous or occasionally with short hairs, the former to ca. 20 mm long (longer in fruit than in flower), the latter often only 0.5-2 mm long (sometimes 3 mm or more in fruit) ; the ultimate bracts  $\pm$  linear, usually  $<$  1 mm long. Flowers fragrant, 5-merous, heterodistylous ; calyx with a short basal tubular portion (often ca. 0.5 mm high), lobes triangular or tooth-like, mostly ca. 0.1-0.5 mm long, glabrous or occasionally with very short hairs on the margins. Corolla tube creamy-white, whitish or yellowish-green, lobes yellow, orange-yellow, reddish-yellow, orange or red ; tube 2-4.5 mm long, funnel-shaped, ca. 0.5-1.1 mm wide at the base, ca. 1.3-1.7 mm wide above in short-styled and to ca. 2.2 mm in long-styled flowers, glabrous outside, often very densely pilose in the throat, particularly in long-styled flowers ; lobes oblong, 1.5-2.7(-3)  $\times$  0.6-1.2 mm,  $\pm$  spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. 3-5 mm in short-styled flowers ; anthers ca. 1-1.2 mm long. Style plus stigmas 7-11 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers ; the exerted, filiform stigma lobes of long-styled flowers ca. 1-2(-2.5) mm long. Ovary subglobose, ca. 0.6-0.8 mm long, glabrous or sometimes with short hairs.

Capsule rather thin-walled, subglobose, ca. 4-6.5(-7.5) mm in diam., glabrous or glabrescent, the valves  $\pm$  sulcate. Seeds yellowish to dark brown, 1.5-3(-3.5) mm in diam., with a broad irregularly lacerate circumferential wing. — B & P - Fig. 4, A ; 7, E ; 12, A-C.

Pollen : 3(-4)-colporate ; average diam. : 11-18  $\mu$ m. (B & P - Fig. 15, A-F).

**ECOLOGY AND PHENOLOGY :** In eastern coastal and lowland rain forest (“forêt orientale”), in forests in the transition zone high plateau - Eastern Domain, in or at the edge of forest remnants of the Central Plateau, in high altitude forest; also associated with dry forest, including forests of the western slopes of the Central Plateau (dry rocky slopes); occasionally in secondary savoka vegetation. — Alt. : 0-1700(-1850) m. — Flowers July, September-May; fruits from all year round except January.

**DISTRIBUTION (Fig. 11, D) :** Widely distributed in Madagascar, also on Mauritius and Réunion.

**CRITICAL REMARKS :** *D. fragrans* is the most widely distributed Malagasy species of *Danais*, occurring in a wide range of rather diverse (although basically forest) habitats. It is also one of the most variable species in the genus : the variation primarily concerns leaf shapes, sizes and texture, inflorescences (congested to somewhat elongated), and seed and also fruit size. Typically, however, the species has thick, coriaceous leaves. Another good characteristic is the calyx of *D. fragrans* : it has a short, yet distinct basal tubular part which bears usually short to very short, often tooth-like lobes.

Malagasy *D. fragrans* does differ from Mascarene material in some character states. Notably, the corollas and fruits of collections from Mauritius and Réunion show some disagreement (the corollas tend to have longer tubes than in Malagasy collections, the fruits are often smaller). In general, however, the collections are not so different as the measurements given by VERDCOURT (1989) suggest. A taxonomic recognition of two geographic entities (e.g. a Malagasy and a Mascarene subspecies) would be a matter of personal taste; in our opinion, there is not sufficient justification for it.

*D. fragrans* is undoubtedly rather closely allied to *D. cernua*; see there for further comments.

**MATERIAL EXAMINED. — MADAGASCAR :** Antsiranana Prov., Montagne d’Ambre (Ambohitra Nat. Park) [S 12.31, E 49.10], Phillipson 1967 (MO, P); Nosy-bé [S 13.20, E 48.15], Boivin 2067 (P), Hildebrandt 3004 (BM, M, P, W), 3346 (BM, K, M, P, W), Pervillé (“voyage Boivin”) s.n. (P), Réserves Naturelles Mad RN 2727 (P); Ampasindava peninsula, mt. massif SW of Ambaliha [S 13.40, E 48.00], Jacquemin 542 (P); 7-10 km E Antsahabe [S 13.40 c, E 48.38], Gentry 11550A (MO); Ambilobe Distr., Mahavavy valley, N of Inanambato, Marivorahona [S 13.42, E 49.06], Humbert 25594 (P); Sambirano, Manongarivo massif [S 14.00 c, E 48.25 c], Perrier de la Bâthie 3826 (P); Ambanja Distr., Marovato Canton, R.N. IV [S 14.00 c, E 48.50 c], Réserves Naturelles Mad RN 4168, 4382 (both P); Beraty, around Maromandia [S 14.01, E 48.15], Decary 1600, 1608 (both P); N of Maromandia [S 14.10, E 48.06], Decary 14855 (P); Maromandia Distr., Bejofo [S 14.14, E 48.20], Decary 2205 (P); Andapa [S 14.39, E 49.39], Réserves Naturelles Mad RN 7985 (P × 2); from Antsohihy to Bealanana, 17-19 km E of Antsahabe [S 14.46, E 48.32], Gentry 11751 (MO); Marosaina, Antalaha [S 15.25, E 50.22], Réserves Naturelles Mad RN 7093 (P); Masoala Peninsula, ca. 6 km NNE of Ambanizana [S 15.34, E 50.00], Schatz & Modeste 2891 (K, MO), 2896 (K); Masoala peninsula, Antalavia [S 15.46, E 50.01], Nicoll et al. 558 (K, MO, P); Mandritsara [S 15.50, E 48.49], Herb. Jard. Bot. Tana 45 (P); upper Bemarivo basin, Amberimay [S 16.30 c, E 48.15 c], Perrier de la Bâthie 3615 (P); Analamahitso forest, Perrier de la Bâthie 3620 (P); Sainte-Marie [S 16.50, E 49.55], Bernier 143 (P), Boivin 1772 (P), Boivin s.n. (BM, P × 2), Jacquemin 383 (P); camp 20 km W of Andilamena [S 17.00 c, E 48.28 c], Cours 1658 (P); 4 km N of Mahambo, between Fenerive and Foulpointe [S 17.28, E 49.27], Gentry 11351 (MO); Foulpointe [S 17.41, E 49.31], Decary 16960 (P); Zahamena, R.N. III [S 17.40 c, E 48.45 c], Decary 16512 (P); Mangabe, Tamatave Distr. [S 17.44, E 49.13], Decary 16878 (P); Ambatondrazaka Distr., Manaka[mbahiny] Canton [S 17.46 c, E 48.40 c], Réserves Naturelles Mad RN 1949, 10469, 11314 (all P); Maheriara [S 17.50, E 48.25], Service Forestier

*Mad SF 10544* (P); Lac Alaotra [S 17.50 c, E 48.25 c], *Herb. Jard. Bot. Tana 3837, 3840, 3854, 3858, 3868, 3874* (all P); P.K. 181, Tampoketsa [d'Ankazobe] [S 17.53 c, E 47.03 c], *Jacquemin 1240, 1241, 1242, 1244, 1245* (all P); Ambatohanaranana, nr. Antsevabe [S 17.58, E 48.32], *Cours 4106* (P); Rombevava massif, [NE of] Bemainty [S 17.58, E 48.45 c], *Cours 4156* (P); Manerinerina, Tampoketsa between Ikopa and Betsiboka [S 18.01, E 47.09], *Perrier de la Bâthie 16854* (P); Manankazo, NE of Ankazobe [S 18.09, E 47.12], *Perrier de la Bâthie 3862, 3884* (both P); Ambohitantely, NE of Ankazobe [S 18.12, E 47.17], *Perrier de la Bâthie 3575* (P); Tampoketsa d'Ankazobe [S 18.20 c, E 47.15 c], *Decary 14374* (P); 7 km E Anjozorobe [S 18.22, E 48.00], *Lowry & Randrianasolo 4422* (MO, P), *Schatz et al. 1389* (BR, MO, P, S); Analabe, N of Antananarivo [S 18.32, E 47.52], *Bosser 5098* (P); Ankazondandy [S 18.42, E 47.47], *Boiteau 79* (P); Anivorano [S 18.44, E 48.58], *Herb. Jard. Bot. Tana 6225* (P); route Tananarive-Moramanga, PK 96 [S 18.53 c, E 48.07 c], *Bosser 13062* (P); [La] Mandraka, PK 69, route Antananarivo-Toamasina [S 18.55, E 47.56], *Barnett & Dorr 204* (BR, MO), *Benoist 1620, s.n.* (both P), *Herb. Jard. Bot. Tana 3678, 3695* (both P), *Keraudren 1134* (P); 27 km E of Beforona, 47 km W of main N-S road jct. [S 18.55 c, E 48.50 c], *Gentry 11272* (K, MO); Analamazaotra forest [S 18.56, E 48.25], *Boiteau 125 D, 510* (both P), *Herb. Jard. Bot. Tana 2150, 3726* (both P); Perinet [S 18.56, E 48.25], *Benoist 1217* (P); Befoza nr. Perinet, *Service Forestier Mad SF 2614* (P); Masse nr. Perinet, *Service Forestier Mad SF 2618* (P); Sakamaloto [S 18.56, E 48.25], *Service Forestier Mad SF 3287* (P); Toamasina Prov., ca. 12 km from Andasibe (Perinet), private forest (Graphite Mine property) [S 18.53, E 48.27], *Puff, Igersheim & Rajemisoa 850823-1/5* (TAN, WU); NE of Graphite Mine, *Phillipson 2137* (MO); around Moramanga [S 18.57, E 48.13], *Decary 17907* (P); Lakato, *Decary 18267* (P); S of Moramanga, *Decary 6916* (BR, P), *Decary 6940* (W); Beforona [S 18.58, E 48.35], *Decary 18009* (P); Antanamalaza [S 18.59, E 47.41], *Herb. Jard. Bot. Tana 3527* (P); around Antananarivo, PK 22 on rd. to the South [S 19.04 c, E 47.33 c], *Bosser 9682* (P); Anosibe-Moramanga rd. [S 19.15 c, E 48.15 c], *Bosser 17849* (P); around Tsinjoarivo [S 19.37, E 47.40], *Humbert 11189* (P); Amboangy-Imady [S 20.30, E 47.20], *Razafindrambao 263* (P); around Ambositra, Mt. Vatomany [S 20.31, E 47.15], *Humbert & Swingle 4755* (P); Sakaleona valley [S 20.35 c, E 48.25 c], *Decary 14174* (P); Tanala [S 20.43, E 47.26], *Deans Cowan s.n.* (BM); Mananjary [S 21.13, E 48.20], *Geay 7233* (P); Ranomafana, between Fianarantsoa and Ifanadiana [S 21.15, E 47.28], *Bosser 345, Phillipson 2177* (K, MO); Mt. Vatovavy, Mananjary [S 21.24, E 47.56], *Decary 13729* (P); Fianarantsoa Prov., Ampantsakambe PK 474, N7, Ambalavao-Ihosy [S 21.50, E 46.50], *Mabberley 1017* (K); around Ambohimahasina, Inaninoma (?spelling) mt. [S 21.56, E 47.11], *Herb. Jard. Bot. Tana 4709* (P); Ambalavao Distr., Sendrisoa Canton [S 22.00, E 46.57], *Réserves Naturelles Mad RN 8505* (P); Manakara Canton, Maro[h]ala, Belambo forest [S 22.07, E 47.56], *Service Forestier Mad SF 16243* (P); Farafangana Prov., Befotaka [S 23.49, E 46.59], *Decary 4745* (P); Ivakoany massif [S 23.50, E 46.25], *Humbert 7028, 12152* (both P); Esetra forest [S 24.28, E 47.12], *Jacquemin 1282* (P); Fort Dauphin Distr., Enaniliha Canton [S 24.40, E 46.52], *Réserves Naturelles Mad RN 8375* (P); Ibakika [S 24.43, E 47.09], *Decary 11058* (P); 22 km N Ifarantsa and ca. 30 km N of RN 13, border of R.N. XI (Andohahela) [S 24.47, E 46.52], *Lowry et al. 4456* (K, MO); Ifarantsa Canton, R.N. XI [S 24.56, E 46.52], *Réserves Naturelles Mad RN 5153* (P); Antorendrika R., towards Bela Venara, ca. 22 km NE Fort Dauphin [S 24.52, E 47.07], *Rabevohitra 1771* (K, MO); Fort Dauphin [S 25.02, E 47.00], *Cloisel 77* (BM), 238 (BM, P); Manantantely forest, *Humbert 20363, 20383* (both P). — Imprecise localities: Itinéraire de Didy [S 18.07, E 48.32] à Brickaville [S 18.49, E 49.04], *Cours 4780* (P); between Tamatave and Antananarivo, *Meller s.n.* (K, P). — Not traced: An°miadilobe-Ambalavao, *Réserves Naturelles Mad RN 9187* (P); Imerina-Nord, Andrainarivo forest, *Campeon 7887* (P); forest N of Nickelville (?), along Ankotirano R., *Cours 2087* (P); Mataniro to Marosika, *Deans Cowan s.n.* (BM). — No locality given (or only "Central Madagascar" or "chiefly from North-West Madagascar"): *Baron 1343* (K, P), 2425, 3895, 5290, *s.n.* (all K), 3894 (P); *Boivin s.n.* (P); *Boivin s.n. (?1201)* (W); *Chapelier s.n.* (P); *Decary 17001* (P); *Homolle 48, 59, 181 bis, 189, 194, 1787, 1819, 2087, V5* (all P); *Humblot 36, 397* (both P, W); *Pervillé 237* (P); *Thompson 135* (BR).

## 24. *Danais cernua* Baker

J. Bot. (London) 20 : 137 (1882); DRAKE in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : tab. 452 (1898); BOITEAU, Bull. Acad. Malg. 24 : 7 (1941).

— *Danais gerrardi* BAKER, J. Linn. Soc. (Bot.) 20 : 160 (1883). Types : *Gerrard 162*, Madagascar, without locality (lecto-, K!, selected here); *Baron 1464*, [nr. A(na)lamazaotra forest] (syn-, P!); *Baron 1536*, [between Tankay and the east coast] (syn-, K!).

— *Danais ternata* BAKER, J. Linn. Soc. (Bot.) 20 : 162 (1883). Type : *Gerrard 12*, Madagascar, without locality (holo-, K!).

— *Danais cernua* BAKER var. *ternata* (BAKER) BOITEAU, Bull. Acad. Malg. 24 : 7 (1941) [not validly published; no reference to basionym].

TYPES : Madagascar, chiefly in Betsileo-Land ["forests of the Tanala country"], *Baron 189* [holo-, K (as "189 ex parte")!; iso-, P-fragm.!]; without locality, *Gerrard 88* (para-, K!).

Woody lianas or climbing shrubs with branched stems to 3(-?) m long, glabrous or sometimes puberulous when young, occasionally lenticellate; stems and leaves sometimes foetid when crushed. Leaves decussate or sometimes also in whorls of 3; leaf-blades membranous to very thinly coriaceous, ovate, obovate, oblanceolate or elliptic, (25-)35-70(-90) × 15-35(-40) mm, acute to (shortly) acuminate at the apex, (gradually) narrowed to the base, mostly glabrous above and below, sometimes midrib below with short hairs, seldom entire lower surface a little hairy; petioles 4-10 mm long, glabrous or sometimes with short hairs; stipules triangular to deltoid, ca. 1-2.5(-3) mm long, [often] with 2 [very, indistinct] teeth at the apex. <sub>not so</sub>

Inflorescences predominantly in the axils of foliage leaves, flowers several to ± many in often subsessile, rather congested clusters (sometimes more elongated in fruit); occasionally also a terminal inflorescence present; peduncles and pedicels mostly glabrous, the former to ca. 10 mm long (longer in fruit than in flower), the latter often only 1-2.5 mm long (sometimes to 4 mm in fruit); the ultimate bracts linear-lanceolate, to ca. 1 mm long. Flowers 5-merous, heterodistylous; calyx lobes narrowly lanceolate to triangular, often ca. 1-3 mm long, occasionally < 1 mm long, erect to ± spreading, glabrous or, more uncommonly, with very short hairs on the margins. Corolla tube greenish-white or yellowish (? also mauve), lobes yellow, orange-yellow, orange or red-orange; tube (4-)5-9 mm long, (narrowly) funnel-shaped, ca. 0.4-0.6 mm wide at the base, ca. 1-1.7 mm wide above in short-styled and to ca. 2 mm in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes oblong, 2-3.3 × 0.8-1.5 mm, ± spreading, glabrous. Stamens included in long-styled flowers but exerted for ca. 3-4.5 mm in short-styled flowers; anthers ca. 1-1.5 mm long. Style plus stigmas 8-13 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exerted, filiform stigma lobes of long-styled flowers ca. 1.5-2.5 mm long. Ovary subglobose, ca. 0.7-0.9 mm long, glabrous or occasionally puberulous.

Capsule rather thin-walled, subglobose, ca. 4-8(-9) mm in diam., or sometimes somewhat wider than high (then often laterally indistinctly compressed), glabrous, the valves occasionally ± sulcate. Seeds brown, 1.7-2.5(-3) mm in diam., with a broad irregularly lacerate circumferential wing. — B & P - Fig. 3, C.

Pollen : 3(-4)-colporate; average diam. : 10-16 μm.

**ECOLOGY AND PHENOLOGY :** In eastern lowland rain forest (“forêt orientale”), in forests of the Central Plateau, in sclerophyllous forest of the western slopes (over gneiss), in mossy high altitude forest (“forêt à mousses”); occasionally in rocky sites (rocky slopes, deep rocky gorges with forest remnants), at the edge of swampy areas (E coast), and also in disturbed or secondary vegetation such as savoka. — Alt. : 0-1500(-1800) m. — Flowers from all year round except July; fruits August-September, December-April, June.

**DISTRIBUTION (Fig. 11, E) :** Endemic to Madagascar. Widely distributed and occurring from the North(east) to the extreme Southeast (Fort Dauphin distr.).

**CRITICAL REMARKS :** Like the preceding species (*D. fragrans*), *D. cernua* is another common and widely distributed Malagasy species of *Danais*. It is fairly variable in vegetative characters (leaf sizes and shapes; leaf arrangement) and, to some extent, also in fruit size. Apart from calyx shape and size, floral features are relatively stable.

*D. cernua* and *D. fragrans* have frequently been misidentified. The former is, however, normally easily distinguished by its thinnish, never thickly coriaceous leaves and also by its larger flowers (longer corolla tubes). Calyx sizes of the two species overlap, but *D. cernua* typically has longer lobes and the calyx lacks a basal tubular part.

It has been noted that in some collections of *D. cernua* the stipules are sometimes shortly bifid at the apex. Such specimens should not to be confused with *D. andribensis*; in the latter the two apical appendages of the distinctly bifid stipules are much longer. Because of major disagreements in various other character states (calyx, corolla tube lengths, leaves, etc.), a close relationship between the two species is rather unlikely.

**MATERIAL EXAMINED. — MADAGASCAR :** Doany Distr., Ambatonaondy [S 14.22, E 49.31], *Réserves Naturelles Mad RN 9095* (P); Ambohitralanana Canton, R.N. II [S 15.14, E 50.27], *Réserves Naturelles Mad RN 3386, 4950, 5712, 10753* (all P); Analamahitso, upper Bemarivo basin [S 16.30 c, E 48.15 c], *Perrier de la Bâthie 3728* (P); around Fenerive [S 17.22, E 49.25], *Perrier de la Bâthie 3898* (P); Sahamaloto, W of Lac Alaotra [S 17.25, E 48.19], *Bosser 8123* (P); ca. 5 km S of Foulpointe, R.N. V [S 17.41, E 49.31], *Barnett & Dorr 250* (MO); Menaloha [S 17.42, E 48.29], *Cours 2687* (P); Ambatondrazaka Distr., Manaka[mbahiny] Est Canton [S 17.46, E 48.40], *Réserves Naturelles Mad RN 11032* (P); Lac Alaotra [S 17.50 c, E 48.25 c], *Herb. Jard. Bot. Tana 3857* (P); PK 45, route no. 5, between Tamatave and Fenerive [S 17.45 c, E 49.27 c], *Croat 32486* (MO); Tamatave Distr., Anjiro [S 17.49, E 49.06], *Réserves Naturelles Mad RN 7711* (P); Ambodiriana, right bank of river [S 17.56, E 49.17], *Cours 1949* (P); NW of Ankazobe, Ikopa valley [S 18.10 c, E 46.58 c], *Decary 7579* (BR, K, P); Anivorano [S 18.44, E 48.58], *Herb. Jard. Bot. Tana 6226* (P); Anivorano, mt. SE of Lohariandava [S 18.48, E 48.41], *Viguiier & Humbert 658* (P × 2); Menalamba [nr.] Perinet [S 18.53, E 48.23], *Service Forestier Mad SF 3311* (P); Mt. Angavokely [S 18.55, E 47.42], *Humbert 20861* (P); nr. A[na]llamazaotra forest [S 18.56, E 48.25], *Baron 1464* (P); Beforona [S 18.58, E 48.35], *Decary s.n.* (P); Hiaranandriana, nr. Behenjy [S 19.12, E 47.29], *Herb. Jard. Bot. Tana 4180* (P × 2); NW Behenjy, Antananarivo-Antsirabe rd., *Dorr et al. 4566* (MO, P); rocher d'Iaranandriana, PK 38, route Antsirabe-Behenjy, *Dorr et al. 2894* (K, MO, P); ca. 8-12 km W of Ambohimadana, on road to Andramasina [S 19.15, E 47.43], *Puff, Igersheim & Rajemisoa 850825-1/4* (TAN, WU); around Vatomandry [S 19.20, E 48.59], *Bernard s.n.* (P); Vatomandry-Andévorante rd., *Guillot 54* (P); Ankaratra [S 19.22, E 47.18], *Scott Elliot 1987* (K); Mania basin [S 19.45 c, E 45.50 c], *Perrier de la Bâthie 12557* (P); Mt. Vontovorani [Vontovorona] nr. Antsirabe [S 19.54, E 47.13], *Perrier de la Bâthie 3510* (P); Ibity [S 20.08 c, E 47.01 c], *Herb. Jard. Bot. Tana 5132* (P); 39 km N Ambositra, route no. 7 [S 20.15 c, E 47.20 c], *Croat 29469* (MO); Analatery-Ambositra [S 20.31, E 47.15], *Razafindrambao 174* (P; mixed with *D. aurantiaca*); Ambositra [S 20.31, E 47.17], *Decary 15108 bis, 15109* (both P); S of Ambositra, *Scott Elliot 2011* (BM, K); Imerina-Imady; route



Ambositra-Ambohimanga [S 20.32, E 47.20], *Peltier & Peltier* 1235 (P); Sakaleona valley [S 20.35 c, E 48.25 c], *Decary* 14244 (P); Tanala [S 20.43, E 47.26], *Baron* 189 (K, P); Ambohimahaso Distr., Ambalamanakana [S 20.44, E 47.55], *Schlieben* 8207 (BM, K); Maroamalona, 15 km from Ambohimahaso [S 21.05, E 47.10], *Razafindrambao* 692 (P); Valozoro, *Decary* 17430, 17477 (both P); Angavoaha, W of Tsitondroina massif [S 21.52, E 47.10], *Herb. Jard. Bot. Tana* 4833 (P); Ambalavao Distr., Mahazony Canton [S 21.59, E 47.02], *Réserves Naturelles Mad RN* 8504, 9187 (both P); Farafananga Distr., Ivongo Canton [S 22.30, E 47.02], *Réserves Naturelles Mad RN* 8521 (P); Ambatomboay [S 22.15, E 47.01], *Réserves Naturelles Mad RN* 9267 (P); Ambondrombe Mt. [S 23.22, E 46.20], *Herb. Jard. Bot. Tana* 4568 (P); Andohahela massif, below Pisopiso (Beaka) [S 24.4?, E 46.4?], *Humbert* 13675 (P); mts. betw. Andohahela and Elakelaka, Vatazo (S of Imonty), *Humbert* 14081 (P); Fort Dauphin Distr., Enaniliha Canton [S 24.40, E 46.52], *Réserves Naturelles Mad RN* 8360 (P); Fort Dauphin [S 25.02, E 47.00], *Decary* 9771, 9838 (both P), *Scott Elliot* 2452 (BM, K), 2667 (K; as anon. coll. 2667 in P but undoubtedly a duplicate collection), 2730 (P); Manantantely forest, *Boiteau* 3072 (P); Pic St. Louis, *Decary* 9962 (P). — Imprecise localities : between Tamatave and Tananarive, *Guillardet* 117 (P); between Andilamena [S 17.01, E 48.35] and Mandritsara [S 15.50, E 48.49], *Perrier de la Bâthie* 15059 (P). — Not traced : Prov. Betani-mena, *Bojer s.n.* (M; W, mixed with *D. microcarpa*); Mataniro to Marosika, *Deans Cowan s.n.* (BM × 2); Imitso forest, *Razafindrambao* 770, 799 (both P). — No locality given (or only "Central Madagascar") : *Baron* 1536, 2454, *s.n.* (all K), 4259, 5954 (both K, P); *herb. Blackburn s.n.* (K); *Bojer s.n.* (P); *Chapelier s.n.* (P × 5); *Cours* 1831 (P); *Decary* 14356, 17308, 17520 (all P); *Gerrard* 12, 88, 162 (all K); *Goudot s.n.* (P); *Herb. Jard. Bot. Tana* 3440 (P); *Homolle* 60, 96, 492, 1949 (all P); *Humblot* 660 (K, P, W); *le Myre de Vilers s.n.* (P); *Thomson s.n.* (BM × 2); *Vaillant* 85 (P); *anon. coll.* 28 (P).

25. **Danais distinctinervia** Homolle. — Fig. 12, A-B.

Not. Syst. (Paris) 5 : 283 (1936); BOITEAU, Bull. Acad. Malg. 24 : 9 (1941).

TYPE : *Perrier de la Bâthie* 3537, Madagascar, Est du Mont Bezofa, vers Vohémar (holo-, P!).

Woody lianas or climbing shrubs, lengths of the stems unknown; young parts glabrous or occasionally puberulous, lenticellate. Leaves decussate; leaf-blades membranous to very thinly coriaceous, elliptic-lanceolate, (55-)85-120 × (20-)30-55 mm, acute at the apex, gradually narrowed to the base, glabrous above and below or midrib below a little hairy; petioles (7-)10-20 mm long, glabrous; stipules triangular, to ca. 2 mm long.

Inflorescences predominantly in the axils of foliage leaves, flowers ± many in rather congested clusters ca. 30 mm in diam.; sometimes also a terminal inflorescence present; peduncles and pedicels puberulous to glabrous, the former to ca. 10 mm long, the latter often only 1.5-2 mm long; the ultimate bracts linear-lanceolate, often < 1 mm long. Flowers 5-merous, heterodistylous; calyx lobes triangular, ca. 0.3-0.5 mm long, erect to ± spreading, glabrous. Corolla tube whitish, lobes orange or red-orange; tube 5-8.5 mm long, narrowly funnel-shaped, ca. 0.4-0.6 mm wide at the base, ca. 1-1.2 mm wide above in short- and in long-styled flowers, glabrous outside, pilose in the throat, particularly in long-styled flowers; base of tube with splits; lobes oblong, 2-3 × 0.5-0.9 mm, ± spreading, glabrous. Stamens included in long-styled flowers but exserted for ca. 3 mm in short-styled flowers; anthers ca. 1 mm long. Style plus stigmas 10-12 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers; the exserted, filiform stigma lobes of long-styled flowers ca. 2-2.5 mm long. Ovary subglobose, ca. 1 mm long, glabrous.

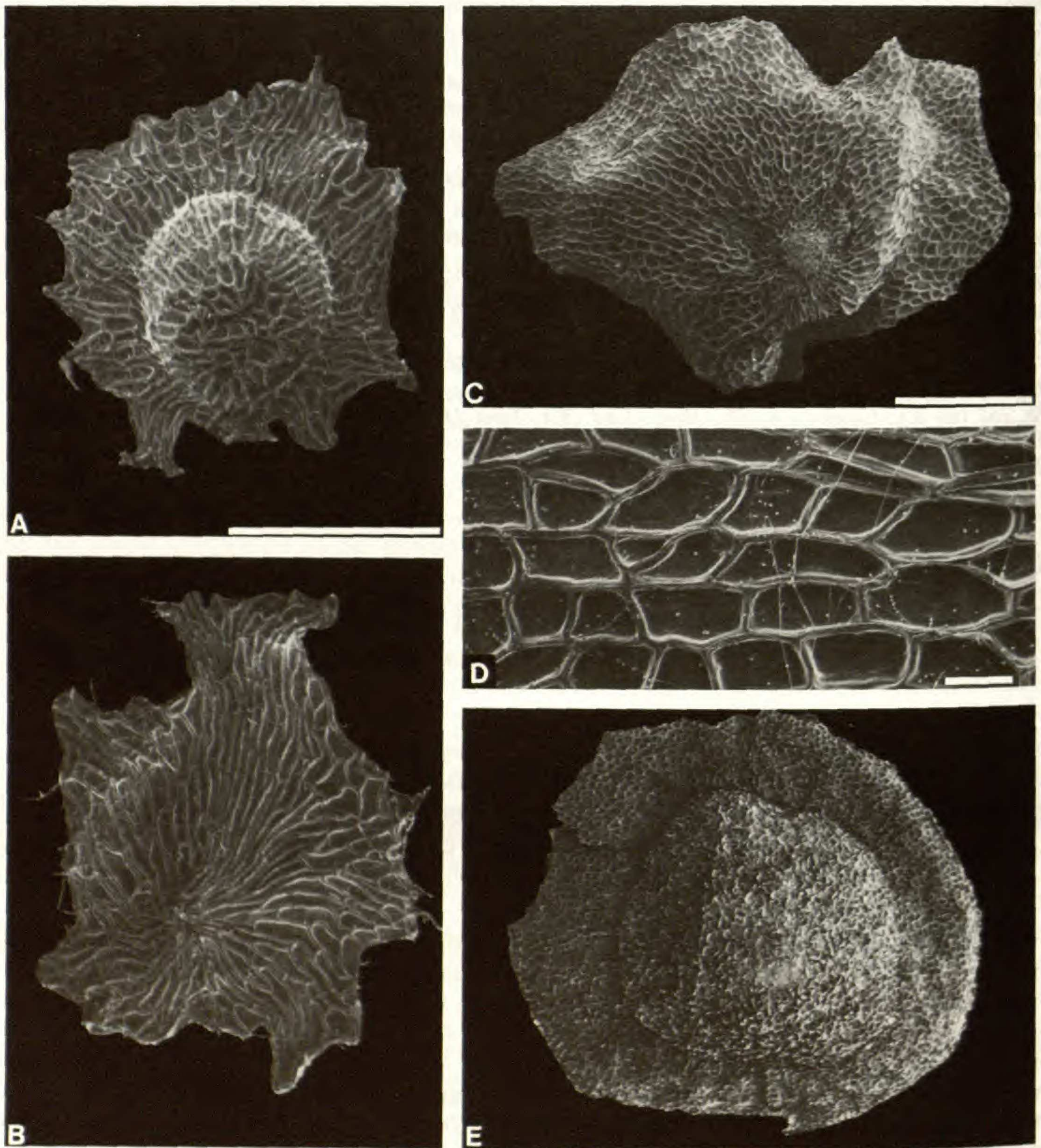


Fig. 12. — Seeds of *Danais* species. — A-B, *D. distinctinervia* (Perrier de la Bâthie 3537, P); A, from above; B, from below. — C-D, *D. pauciflora* (Baron 1298, P); C, from below; D, detail of seed wing. — E, *D. volubilis* (Humblot 11204, P), from above. — Scale bars : 1 mm (C = E); 0.5 mm (A = B); 100  $\mu$ m (D).

Capsule thin-walled, subglobose, ca. 4-7 mm in diam., glabrous, the valves  $\pm$  sulcate. Seeds brown, 1-1.4 mm in diam., with an irregularly lacerate, sometimes  $\pm$  elongated circumferential wing.

ECOLOGY AND PHENOLOGY : No information on habitats available. — Alt. : ?-300-? m. — Flowers July ; fruits July.

DISTRIBUTION (Fig. 11, *F*) : Endemic to Northeast Madagascar.

CRITICAL REMARKS : *D. distinctinervia* is likely to be a close ally of *D. cernua*. Both species are characterized by having thinnish leaves (the leaf-blades of *D. distinctinervia*, however, are larger than those of *D. cernua*), and corolla tube and fruit sizes overlap. Seed size provides a good distinction character (considerably smaller in *D. distinctinervia* than in *D. cernua* ; cf. Fig. 4, *B*).

MATERIAL EXAMINED. — MADAGASCAR : E of Mt. Bezofa, towards Vohémar [S 13.20 c, E 50.00 c], *Perrier de la Bâthie* 3537 (P). — Imprecise locality : between Vohémar and Ambilobe, *Decary* 14641, 14647, 14751 (all P).

## 26. *Danais hispida* Baker

J. Linn. Soc. (Bot.) 20 : 161 (1883) ; BOITEAU, Bull. Acad. Malg. 24 : 8 (1941).

TYPE : *Baron* 1304, Madagascar, without locality (holo-, K! ; iso-, K!).

Presumably woody lianas or climbing shrubs [no data available] ; stems dark brown, mostly with light grey-brown lenticels, densely to very sparsely covered with greyish to brownish long multicellular hairs, sometimes  $\pm$  glabrous. Leaves decussate ; leaf-blades  $\pm$  membranous, ovate, obovate or broadly elliptic, 45-125  $\times$  25-70 mm, acute to (shortly) acuminate at the apex, cuneate to  $\pm$  rounded at the base, hairy above and below or upper surface glabrous and a few hairs on the veins below ; petioles 5-10(-12) mm long, hairy to  $\pm$  glabrous ; stipules rounded to  $\pm$  deltoid, 3-8  $\times$  4-6 mm, margins with long greyish-white multicellular hairs.

Inflorescences in the axils of foliage leaves, flowers several to  $\pm$  many in somewhat congested clusters ; peduncles and pedicels glabrous or a little hairy, the former to ca. 5 mm long, the latter 1 mm or less long ; ultimate bracts linear-lanceolate, often  $<$  1 mm long. Flowers 5-merous, heterodistylous ; calyx with a very indistinct basal tubular part, lobes narrowly triangular, ca. 0.5-0.6 mm long, erect to  $\pm$  spreading, margins ciliate to subglabrous. Corolla colour unknown ; tube 3.5-6 mm long, narrowly funnel-shaped, ca. 0.6 mm wide at the base and ca. 1.2 mm wide above in short-styled and ca. 1.4 mm in long-styled flowers, glabrous outside, hairy in the throat, particularly in long-styled flowers ; lobes oblong, ca. 1-2  $\times$  0.5 mm, glabrous. Stamens exerted for ca. 4 mm in short-styled flowers ; anthers ca. 1 mm long. Style plus stigmas 7-10 mm long in long-styled flowers, shorter than the corolla tube in short-styled flowers ; the exerted, filiform stigma lobes of long-styled flowers ca. 2-3 mm long. Ovary subglobose, ca. 1 mm long, glabrous to a little hairy.

Capsule  $\pm$  thin-walled, subglobose, 5-6 mm in diam., glabrous. Seeds dark brown, ca. 2 mm in diam., with a broad irregularly lacerate circumferential wing. — B & P - Fig. 3, *B*.

ECOLOGY AND PHENOLOGY : In or at the edge of forest over gneiss ; no further detailed information available. — Alt. : 1000-1440 m. — Flowers January ; fruits : no dates given.

DISTRIBUTION (Fig. 11, *F*) : Endemic to Madagascar ; confined to the Central Plateau area.

CRITICAL REMARKS : Only known from three collections from the late 19th century and one from 1955 (*Humbert & Capuron 28502*). As *D. hispida* seems to be confined to the heavily destroyed Central Plateau area it is possible that the apparently rare species is now extinct.

The known collections vary in their stem and leaf indumentum, ranging from very dense to almost absent. This variation, however, does not effect the stipules ; their margins are always beset with rather long, multicellular hairs.

*D. hispida* appears to be very close to the widely distributed *D. cernua*. In certain character states (e.g. leaf texture and shape, floral characteristics), it approaches the latter.

MATERIAL EXAMINED. — MADAGASCAR : Ambohimombo forest, Tanala [S 20.43, E 47.26], *Forsyth-Major 298, 357* (both BM) ; Andrambovato, E of Fianarantsoa [S 21.26, E 47.05], *Humbert & Capuron 28502* (P). — No locality given, *Baron 1304* (K × 2).

## IMPERFECTLY KNOWN SPECIES

### **Danais comorensis** Drake

Bull. Soc. Bot. France 45 : 348 (1898, publ. 1899) ; BOITEAU, Bull. Acad. Malg. 24 : 7 (1941). — “*Danais comorensis* DRAKE ex CAVACO, *Adansonia*, sér. 2, 8 : 387 & pl. 1,5-7 (1968)”.

TYPE : *Boivin 3194*, Comores, Mayotte (holo-, P!).

The species is only known from the fruiting type specimen (a second collection cited by CAVACO, 1968, as being *D. comorensis* is in fact *D. longipedunculata*).

Little can be added to CAVACO's (l.c.) redescription (“*Danais comorensis* Drake ex Cavaco”, by the way, is unjustified because DRAKE's original diagnosis is perfectly valid) except that the specimen does not bear terminal but paired axillary inflorescences (this is also seen in his illustration).

It is suspected that the species might just be an odd, pubescent variant of *D. humblotii*. The latter also occurs on the Comores (but hairy variants are neither known from there nor from Madagascar). The species, nevertheless, is formally upheld at present. Flowering material would be needed to draw a definite conclusion on its status.

### **Danawis baronii** [“*baroni*”] Homolle

Not. Syst. (Paris) 5 : 281 (1936) ; BOITEAU, Bull. Acad. Malg. 24 : 6 (1941).

TYPE : *Baron 6607*, Madagascar, “North Madagascar” (holo-, P! ; iso-, K!).

Like the previous species (*D. comorensis*), *D. baronii* is only known from the type, a fruiting collection of which neither a precise locality nor data on habit and habitat are known.

The holotype is a portion of a branch only showing axillary inflorescences, whereas the isotype is comprised of the end piece of a branch with both terminal and axillary inflorescences. Conspicuous are the coriaceous leaves with the reticulate venation being raised and prominent both above and below.

It is suspected that it might be related to *D. humblotii*, from which it however differs in the texture of the leaves and the shape of the inflorescences. Before flowering material becomes available, the status and relationships cannot be determined with certainty.

## UNCERTAIN GENERIC POSITION

The generic position of the following species is uncertain :

### **Danais coerulea** Homolle ex Cavaco

Bull. Mus. Hist. Nat. Paris, sér. 2, 37 : 718 (1966).

TYPE : *Perrier de la Bâthie* 3823, Madagascar, Manongarivo massif (holo-, P!).

The species, described as a shrub<sup>1</sup>, is vegetatively characterized by large, broadly ovate, recurved foliaceous stipules. The inflorescences are congested and head-like, and the corolla tubes are hairy on their outside. In these characters, the species reminds of *Payera*. The inflorescences, however, are borne both axillary and terminal (whereas *Payera* has strictly terminal inflorescences).

Fruits and seeds would be needed to obtain more certainty about its generic position. — In his original description, CAVACO did include data on fruits and seeds ; it, however, is not known where he might have got them from since the type specimen, the only collection known, only bears buds and flowers. In any case, his characterization (“*capsula alba, carnosae, deinde siccae et dehiscentis, lobis calycis coronatae. Semina multa, minuta, alata*”) is too imprecise to be of help.

## TO BE EXCLUDED FROM DANAIS

In addition to the relevant information in BUCHNER & PUFF (1993), a comment is necessary on

“*Danais homolleana* CAVACO” and “*Danais wernhami*”

The two names (both not correctly published) are apparently meant to be nomina nova for one and the same species, namely

1. Based on PERRIER's notes on the type sheet. His characterizations of growth habits are generally precise (as opposed to frequent imprecise and misleading habit descriptions by various other collectors and authors). It is, therefore, considered unlikely that *D. coerulea* is a liana [as would be typical for *Danais*].

*Sabicea verticillata* WERNHAM

Monograph of the genus *Sabicea* : 74 (1914). Type : *Humblot 213*, Madagascar, without locality (holo-, P! ; iso-, BM).

The first name, “*Danais homolleana* CAVACO”, appears on a revision label written by CAVACO and dated “1967” (attached to the type sheet of *Sabicea verticillata* in herbarium P). It is undoubtedly meant to be a *nom. nov.* [because there is a *D. verticillata* BAKER (1883)].

CAVACO might have overlooked that he had previously chosen a different new name, i.e., “*Danais wernhami*”. — The latter is included in his key of *Danais* (CAVACO, 1966) but there is neither an author given nor is there any indication whatsoever that it is meant to be a *nom. nov.* The key characters, nevertheless, leave no doubt that “*Danais wernhami*” also refers to *Sabicea verticillata*.

The problem of a correct *nom. nov.* for *Sabicea verticillata*, however, need not be considered any further. A reinvestigation of the type specimen showed that a transfer of the species to *Danais* is not justified. Handwritten comments on the type sheet (“very young seeds winged”), which probably prompted CAVACO to place the species with *Danais*, are misleading. The specimen only has flowers but no young fruits.

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